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BREEDING FOR DISEASE-RESISTANCE IN CANADA

PART I. CEREALS

C. H. GOULDEN[1] AND T. M. STEVENSON[2] *et al.*[3]

Introduction.—THE concentration and continuation of cereal production in Canada have intensified the problem of disease. For example, after the distribution of Marquis wheat to the prairie provinces (Manitoba, Saskatchewan, and Alberta) wheat-growing became general, and many areas of those provinces became almost a continuous wheat-field. This was particularly conducive to the spread of epidemics of stem rust. In 1916, after Marquis wheat had become fully established, an epidemic of stem rust occurred for which the loss in yield of wheat is estimated at approximately 100 million bushels.

Following the disastrous epidemic of 1916, pressure was exerted on government agencies to put greater emphasis on breeding for disease-resistance. As a result the first concentrated attack on a series of disease problems by the plant-breeding method began about 1925 with the establishment of a laboratory at Winnipeg, where the study of rust and breeding for stem-rust resistance were the main objectives. In this organization from the outset plant-breeders and plant-pathologists co-operated in the breeding problem, and this is the method of attack which has now become general in Canadian institutions.

The facilities for cereal breeding in Canada are located at the various experimental stations of the Dominion Experimental Farms System and the provincial universities. In the Dominion Experimental Farms System breeding work is concentrated at the following points: the Central Experimental Farm, Ottawa, the Dominion Laboratory of Cereal Breeding at Winnipeg, and the Branch Stations at Brandon, Indian Head, Swift Current, Scott, Lethbridge, and Lacombe. The universities concentrating on cereal breeding are: the University of Alberta, at Edmonton; the University of Saskatchewan, Saskatoon; the University of Manitoba, at Winnipeg; the Ontario Agricultural College, at Guelph, Ontario, and Macdonald College at Ste Anne de Bellevue, in Quebec.

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Breeding for disease-resistance in flax, forage plants, tobacco, and horticultural crops will be dealt with in subsequent papers.

Stem rust and leaf rust of wheat.—Stem rust of wheat caused by the fungus *Puccinia graminis tritici* Eriks. and Henn., of which over 200 physiologic races have been identified, has caused the greatest losses in Manitoba and eastern Saskatchewan where destructive epidemics have been frequent. In other wheat-growing areas of Canada considerable damage has also been done. Before 1939 when rust-resistant wheats became generally grown, stem rust was the most destructive of the wheat diseases and very large losses occurred in the years 1916, 1927, and 1935, which were estimated by Craigie [1] at approximately 100 m., 90 m., and 87 m. bu. respectively. For the 11-year period 1925–35 the average annual loss in Manitoba and Saskatchewan was estimated by Greaney [2] to be 35,518,000 bu.

Leaf rust of wheat caused by *Puccinia triticina* Eriks., of which some 130 physiologic races are known, has occasionally caused severe losses in the prairie provinces, but these losses are more difficult to estimate than in the case of stem rust.

Breeding for rust-resistance in the United States antedated the initiation of breeding work in Canada, and varieties from the U.S.A. have made a notable contribution to Canadian agriculture. Ceres, which was introduced first in 1924, was the chief rust-resistant wheat in Canada until 1935, when it succumbed to physiologic race 56 of stem rust. Thatcher wheat, introduced in 1935, still occupies a larger acreage than any other variety in Canada.

In 1916, and for some years following, no rust-resistant varieties of *Triticum vulgare* Vill. were known which might be used as parental material for breeding bread-wheats. It appeared necessary to introduce rust-resistance into *T. vulgare* from other species, such as *T. durum* Desf. or *T. dicoccum* Schubl., by interspecific crosses.

By 1935 several important rust-resistant derivatives developed from interspecific crosses in the U.S.A. were available in Canada as breeding material. A number of strains known as 'Double Cross' had been produced in Minnesota from the double cross (Marquis × Iumillo) × (Marquis × Kanred). These were resistant to stem rust but susceptible to leaf rust. Later, one of them was named Thatcher. Two important varieties, known as Hope and H–44 respectively, had been developed from the cross Marquis × Yaroslav Emmer by E. S. McFadden in South Dakota. Hope and H–44 had mature plant-resistance to the then prevalent races of stem rust and leaf rust, and possessed considerable resistance to both covered and loose smuts. The discovery in 1927 by Goulden, Neatby, and Welsh [3] that the inheritance of stem-rust resistance of H–44 wheat was controlled by a single main factor difference in such crosses as H–44 × Marquis greatly facilitated the breeding work.

Cereal chemists have co-operated with plant-breeders and pathologists to produce disease-resistant wheats of high quality. The following table lists licensed rust-resistant spring-wheat varieties of *Triticum vulgare* developed in Canada:

Variety	*Cross*	*Where originated*	*Year of licence*	*Stem-rust reaction**	*Leaf-rust reaction**
Apex	(H–44 × D.C.†) × Marquis	Saskatoon	1936	R	S
Renown	H–44 × Reward	Winnipeg	1936	R	MR–MS
Coronation	Pentad × Marquis	,,	1938	R	MR–MS
Regent	H–44 × Reward	,,	1939	R	MR–MS
Redman	Regent × Canus	,,	1946	R	MR–MS
Rescue	Apex × S–615	Swift Current	1946	R	S
Saunders	Thatcher × 44·7‡	Ottawa	1947	R	S

* R = resistant; MR = moderately resistant; MS = moderately susceptible; and S = susceptible.

† Double cross.

‡ 44·7 is a rust-resistant derivative of Hope × Reward.

Improved strains of all these seven varieties have been developed for foundation stocks.

All these varieties are still being grown. Regent is at present the main wheat variety in the 'rust area'. Redman is a newer production which is a higher yielder than Regent and has resistance to covered smut, *Tilletia caries* (DC.) Rostr. and *T. foetida* (Wallr.) Liro. Rescue combines sawfly-resistance (due to solid stem) with stem-rust resistance. Saunders is an early maturing wheat adapted to the northern fringe of the wheat-growing area in western Canada.

The breeding of varieties of wheat resistant to stem and leaf rust has therefore been a decided success especially with reference to stem rust, and Craigie [1] has estimated that in Manitoba and eastern Saskatchewan in the six-year period 1938–43 the growing of rust-resistant wheat varieties increased the average annual production by 41·339 m. bu.

A very interesting situation has now arisen in connexion with the discovery of a virulent race of stem rust known as race 15B. This race has occasionally been found in small isolated amounts in the U.S.A. and was collected once in Canada in 1946. It is capable of attacking Hope and H–44 and all common wheats grown commercially in North America.

As soon as this race was discovered active steps were taken to discover resistant parent material. An important gene conferring resistance to race 15B was found to be allelic in the varieties McMurachy, Kenya (R.L. 1373), and Red Egyptian. In addition this gene controls resistance to all races of stem rust so far tested in the rust area of western Canada under field conditions.

Breeding work has been in progress for several years to develop satisfactory wheat having the necessary resistance to race 15B, and now some promising derivatives are available, especially from the back-cross (McMurachy × Exchange) × Redman[3].

Races of leaf rust of greater virulence than those formerly known have also been occurring in western Canada in recent years; they began to appear more frequently from 1945 onward, and they may infect the wheats now being grown in western Canada. In searching for varieties of wheat having resistance to these virulent races a variety known as

Exchange (formerly known as Warden × Hybrid English) was tested and found to be resistant to all the races now generally distributed throughout the prairie provinces, including the most virulent races. In the crosses being made particularly for the development of resistance to race 15B the leaf-rust resistance of the variety Exchange is also being incorporated. The cross mentioned above (McMurachy × Exchange) × Redman[3], is a typical example of one in which the resistance to race 15B of stem rust is being combined with resistance to the more virulent races of leaf rust. Similar work to the above is being done with sawfly-resistant and with early maturing wheats. Genes from derivatives of *Triticum timopheevi* Zhuk. and other new sources are being added.

Breeding for disease-resistant oats.—Among farm crops in Canada the oat crop ranks second to wheat in value; it is grown throughout the country, and in the mixed farming areas of eastern Canada and in British Columbia it occupies an important place in the crop rotation. In the prairie provinces where grain crops represent a high percentage of the total cropped area, oats occupy between 20 and 25 per cent. of this acreage.

Losses to the oat crop in Canada due to disease run into millions of dollars annually. Greaney [2] estimated that between 1929 and 1934 the annual loss from oat stem rust alone in Manitoba and Saskatchewan was over 2 million dollars.

Diseases of oats in Canada that cause the greatest damage are stem rust, crown rust, loose and covered smut, and root rots. Diseases of minor importance are halo blight *Pseudomonas coronafaciens* (Elliott) Stapp. U.C. (S) in Stapp grey speck (manganese deficiency), leaf blotch *Helminthosporium avenae* Eidam, and speckled leaf blotch *Septoria avenae* Frank. Breeding for disease-resistance in oats has been confined largely to the rusts and smuts and a concentrated breeding programme to obtain resistance to these diseases was initiated in 1926. Extensive surveys are conducted annually by the Dominion Laboratory of Plant Pathology, Winnipeg, to obtain information on the distribution of physiological races of rust in Canada.

Before 1925 physiologic races of oat stem rust *Puccinia graminis* Eriks. and Henn. had been identified from only a few collections in Canada. In 1926 oat-rust research was undertaken in an extensive way by the Dominion Laboratory of Plant Pathology, Winnipeg, Manitoba. Races 1, 2, and 5 of stem rust were the common ones isolated at that time, the majority of these being from the prairie provinces. In the early years, even though some attention was given to breeding for crown-rust resistance, it was not considered to be as pressing a problem as breeding for stem-rust resistance. Hence the main objective was to develop stem-rust resistant varieties for areas in Manitoba and Saskatchewan, where the crop was being damaged yearly by stem rust. After 10 years' effort a new variety, Vanguard (Hajira × Banner), was released in 1937 by the Dominion Laboratory of Cereal Breeding, Winnipeg, as the first stem-rust resistant variety developed in Canada. This new variety was quite widely adapted to both eastern and western conditions where stem rust

was destructive. Its resistance to races 1, 2, 5, 3, 7, and 12 came from the Hajira parent.

In eastern Canada crown rust was generally considered to be more prevalent than stem rust, although there were areas where losses from stem rust were severe. Initial surveys showed that races 2 and 3 of crown rust *Puccinia coronata avenae* (Corda. Eriks. & E. Henn.) were the most common throughout Canada. In 1938 the Ontario Agricultural College released the variety Erban (Banner × Early Ripe). This variety was resistant in the mature-plant stage to crown-rust races 2 and 3, and was thus of great benefit to producers in eastern Canada where the variety was found to be best adapted.

Following the introduction of Vanguard and Erban, two new varieties were introduced by the Dominion Laboratory of Cereal Breeding, Winnipeg. Ajax (Victory × Hajira) was introduced in 1942 and Exeter (Victory × Rusota) in 1944. Although these varieties possessed only the same rust-resistance as Vanguard, the former was particularly desirable from the standpoint of early maturity and wide adaptability, whilst the latter was adapted to the northern portions of the stem-rust areas in Manitoba and Saskatchewan.

To provide some combined resistance to both crown and stem rust in eastern Canada, work had been in progress for some years, with the result that two new varieties Roxton and Beaver were released in 1944. Roxton was produced at Macdonald College, Quebec, and had considerable resistance to the prevailing stem- and crown-rust races in eastern Canada. The parentage of Roxton included the varieties Siberian, Joanette, O.A.C. 72, and Early Ripe. Beaver (Vanguard × Erban) was produced by the Cereal Division, Central Experimental Farm, Ottawa. It had the combined resistance of both parents. These varieties have served to offset rust damage in eastern Canada to a considerable degree.

During the years in which Ajax, Exeter, Roxton, and Beaver were being developed additional races of crown rust and stem rust became more common, with the result that these varieties are often quite heavily infected. Although races 2 and 3 continued to be the most prevailing races of crown rust in eastern Canada and 1 and 4 in western Canada, races 1, 2, 3, 4, 5, 6, 24, 34, and 45 were commonly found throughout the country. Races 1 to 6 comprised up to 90 per cent. of the isolates in recent years. In the case of stem rust, the common races of earlier years, namely, 1, 2, and 5, continued to make up approximately 70 per cent. of the oat stem-rust collections in Canada. Races 4 and 6 have caused damage in local areas in some years. However, race group 8, 10, and 11 has been prominent since 1943 and has resulted in heavier rust infections on varieties with the Ajax and Beaver type of resistance.

One of the most notable contributions to oat-breeding in Canada was the production of strains with complete resistance to all known races of stem rust by the Dominion Laboratory of Cereal Breeding, Winnipeg. The original Hajira was heterozygous for stem-rust reaction, certain plants being resistant to races 1, 2, 5, 3, 7, and 12, whilst others were resistant to all races. Plants that were resistant to all races appeared in three hybrid populations, Hajira × Joanette, Hajira × Richland, and

Hajira × Banner. Garry, one of whose parents was the resistant selection no. 524 (Hajira × Banner), represented the first commercial oat variety having resistance to all races of stem rust in Canada.

In the development of varieties resistant to crown rust, the parent variety Victoria has been used extensively by the plant-breeder. Garry, referred to above as being resistant to all races of stem rust, also carries the Victoria resistance to crown rust. It was released in 1947. Another new variety called Beacon was released from the Cereal Division, Central Experimental Farm, Ottawa, in 1946. It also carries the Victoria type of crown-rust resistance. This variety has the Vanguard stem-rust resistance only but has two other characters, earliness and lodging resistance, which are important on the more fertile soils. Both Garry and Beacon proved susceptible to Victoria blight *Helminthosporium victoriae* (Meehan and Murphy), which appeared in Canada in 1947. The damage caused by this disease has curtailed drastically the extent to which these varieties are grown.

The oat-breeding programme in Canada must continue to be directed towards producing varieties with more disease-resistance. The appearance of *H. victoriae* means that all hybrid material susceptible to it must be eliminated. Hybrids having the Bond crown-rust resistance are being used extensively for the present. However, such hybrids are susceptible to race 45 of crown rust, and since this race shows evidence of increasing, one must look to other sources for crown-rust resistance. This is being done by breeding new parental material with the required resistance, and also by using other available varieties having resistance to all common races of crown rust. Some of these are Santa Fe, Klein 69B, Landhafer aus Uruguay, and Trispernia. The increasing importance of race 8 of stem rust in the past few years means that all future hybrids for rust areas must possess resistance to this race. Excellent sources of stem-rust resistance are now available in both standard varieties and hybrid material. Incorporating smut-resistance into hybrid material presents no particular difficulties. It is important, however, that the new varieties possess smut-resistance.

Breeding for disease-resistance in barley.—In Canada the destructive diseases of barley are:

(*a*) Stem rust (*Puccinia graminis*) Eriks. and Henn.
(*b*) Leaf rust (*Puccinia hordei*) Otth.
(*c*) Loose smut (*Ustilago nuda*) (Jens.) Rostr.
(*d*) Covered smut (*Ustilago hordei*) (Pers.) Lagerh.
(*e*) False loose smut (*Ustilago nigra*) Tapke.
(*f*) Helminthosporium spot blotch (*H. sativum*) Pam., King, and Bakke.
(*g*) Speckled leaf blotch (*Septoria passerini*) Sacc.
(*h*) Common root rot (*Helminthosporium* spp. and *Fusarium* spp.).
(*i*) Powdery mildew (*Erysiphe graminis*) DC.

Prior to 1939 stem rust was responsible for heavy losses in the barley crop, but following the widespread introduction of rust-resistant wheats, this disease became considerably less important. However, epidemics

such as that of 1948 may still occur with sufficient frequency to make the production of rust-resistant varieties worth while.

Loose smut is widespread throughout western Canada and is a serious disease of barley in the west at the present time. Very severe infections sometimes occur.

Leaf rust does not assume epidemic proportions more than about once in 8 years. However, in those years considerable damage may result and it is therefore desirable that resistant varieties be developed.

Powdery mildew of barley is most serious in eastern Canada, but some damage occurs in the prairie provinces. A severe epidemic occurred in Manitoba in 1941. In the east, before 1936, this disease occurred only in isolated fields. It first became important in western Ontario and over the years it spread gradually to the eastern part of the province and into Quebec. If the attack occurs early in the season, damage to the crop is quite marked, but as a general rule it occurs only on the late-seeded crops. Under some circumstances in eastern Canada, barley cannot be seeded early and it is in these fields that damage from mildew is likely to occur. In British Columbia damage from mildew occurs nearly every year.

The breeding of stem-rust resistant varieties of barley has been receiving attention since 1937. This work has been concentrated at the Dominion Experimental Farm at Brandon, Manitoba. The first cross made was Newal × Peatland, using Peatland as the source of rust-resistance. Stiff-strawed, rust-resistant selections from this cross were combined with such standards as O.A.C. 21, Mensury Ottawa 60, and Plush. This work has given rise to a number of rust-resistant lines now in yield-tests across the prairies. The newly licensed Vantage barley is one of this group. Vantage is a non-shattering, stiff-strawed, rust-resistant, smooth-awned type of barley.

Breeding work at the present time is concentrated on the development of hybrids resistant to both stem rust and smut with particular reference to *Ustilago nuda* (Jens.) Rostr. A number of improved rust-resistant hybrids referred to above have been used as parental material in crosses with the smut-resistant varieties Titan and Velvon II. The cross Titan × Vantage has provided promising material and many rust-resistant lines exhibiting freedom from smut have been isolated and are now in advanced yield-trials.

Breeding for leaf-rust resistance in barley has been under way for only a few years. Several resistant varieties, including Carre 180, Cebada, Capa, and the University of Wisconsin selection H. 106.1, and Moore have been used as resistant parents. It is as yet too early to make any reliable predictions as to the success of this project.

Research work on powdery mildew of barley was undertaken in 1934 at the Dominion Laboratory of Plant Pathology, in Winnipeg; and in 1939 when a collection of barleys was subjected to a mildew epidemic in the Cereal Division greenhouses in Ottawa, some varieties were found to possess resistance and were used as parents for crosses made in the summer of 1939. Since that date further studies have been made in the same Laboratory on a number of varieties from the U.S.D.A. World

Collection. These varieties have been studied for their resistance to various physiologic races and those showing high resistance are now being used as parents by plant-breeders.

In the early work on mildew resistance the variety Chevron was used as the mildew-resistant parent. However, tests carried out in the greenhouses at Ottawa since 1939 showed this variety to be susceptible to a form of mildew hitherto not reported, so that all crosses based on the resistance of this variety had to be discarded. However, in earlier crosses the variety known as Duplex from the World Variety Collection had been used, and from these crosses several strains were produced all more desirable than the Duplex variety, but still not suitable for commercial use. The best of these are now being used for parent material as well as a number of highly resistant but not agronomically desirable varieties from the World Collection. Particular emphasis is being placed on an unnamed variety originally received from Morocco, which is known in the collection as C.I. 4979. This variety has been reported by Newton and Cherewick [4] as being immune to the 9 physiologic races of powdery mildew important in Canada. The present aim is to add mildew-resistance to the varieties commonly grown in eastern Canada, such as O.A.C. 21, Montcalm, Barboff, and Galore, as well as to the most promising hybrid strains that are in an advanced stage of testing. Unless new physiologic races are found, it would seem to be possible to produce varieties possessing high mildew-resistance under practical field conditions.

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THE RELATION BETWEEN THE SIZE OF FIELDS AND THE SPREAD OF PLANT-DISEASE INTO THEM

PART III. EXAMPLES AND DISCUSSION

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In Part I [1] crowd diseases were discussed: diseases caused by infections that neither persist for long in the soil nor travel far in considerable amount. It was shown that if infection enters a field from its surroundings (e.g., from alternate hosts in the surrounding vegetation), then simple arithmetic shows that the amount of infection entering per acre decreases as the area of the field increases, shape, &c., being constant. If infection moves from field to field, then movement can be reduced by making the fields larger and correspondingly fewer, a deduction that is supported by what relevant experimental evidence there is in the literature. Further, most virus diseases seem to be crowd diseases, this being related to the mode of existence of the viruses. It remains to discuss the subject in relation to some particular problems, most of them African.

Groundnut Rosette Disease; Maize Streak Disease; Aphis-born Virus Diseases of Beet

Rosette disease of groundnuts occurs over much of Africa, often destroying whole crops, and the fear exists that it will menace the great groundnut schemes. Massing groundnuts in units of tens of thousands of acres is courting trouble, some feel, and gives both the virus and its vector the chance to build up to dangerous levels; for, it is argued, the whole experience of plant pathology shows that intensification of cultivation brings with it intensification of disease, and if the disease is as widespread and destructive as it now is, it will surely be many times worse as vast areas go down to nuts and time allows infection to accumulate. This argument is wholly fallacious. Admittedly, intensification of cultivation normally promotes infection, but experience here is valid only for the normal course of intensification, which is by multiplying the number of fields without substantially changing their size. In the new groundnut schemes it is the size of the fields which is conspicuously changed, and this is quite another matter.

The virus is not transmitted by seed, nor does it persist in the soil or dead plant-residues. Moisture permitting, groundkeepers can carry it from season to season, but in large mechanized fields they are easily destroyed, and if they were the only source of virus nothing but slovenly management could allow the virus to become a menace. Unfortunately, however, there is evidence of an alternative source: an indigenous source in the veld. For example, experience has shown that over much of the Transvaal isolated patches of groundnuts, planted in an area for the first time in memory and many miles away from other groundnuts, become

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infected just as quickly as in the main producing areas. Alternate hosts have not been identified. (In the Congo, Soyer [2] found *Centrosema plumeri* to be susceptible, but it was not possible to infect groundnuts from it; nor is Centrosema indigenous to Africa.) But hypothetical as an alternate indigenous host may be, the circumstantial evidence for it is strong, and it must be considered seriously as the only conceivable threat to large fields under competent management. Against such an indigenous source, largeness of field would in itself be the best safeguard. Provided that most of the infection comes from relatively near the edge of the field, the amount of infection received per acre would fall as the size of the field increases (see Fig. 1, Pt. I). With fields of many thousands of acres, 'relatively near' means within several miles, which, by all experience, would seem more than adequate to include the distance covered by aphis-borne viruses coming from scattered plants, as distinct from a concentrated source like a large diseased field (see the paragraph on relativity in isolation on p. 137 of Pt. I). With proper management big fields are therefore likely to be safer just because they are big, and the omens for the new scheme are fair, even in districts where small plots suffer considerably.

The gist of the argument is that experience with viruses indicates that there is little danger to a field from small sources of infection 5 or 10 miles away. If it is found that rosette virus is brought in in quantity from greater distances, it would not alter the conclusion that large fields are safer, but it would reduce the degree to which they are safer.

In making this comparison between big fields and small it is assumed that other things are equal, especially the time and density of planting. Density of planting influences directly the vector population and thus the multiplication of infection within the field—as experience shows [3] —and indirectly, through its influence on the multiplication of infection, the usefulness of the enlargement of fields. With swift multiplication no method of incomplete sanitation—for that is what the enlargement of fields is—is satisfactory. This point is discussed below.

There is an important provision. If it is necessary to intersect large fields with anti-erosion strips, the vegetation in these strips should be above suspicion, or be replaced. If grasses are used, then, to anticipate what follows in the next paragraph, they should be of species immune from streak disease. Another provision is that the planting of a field should be completed in a fairly short time, so that the plants are more or less of an age; for homogeneity in age, as in any other vital respect, is essential if the size of the field is not to affect the rate of multiplication of infection within it (see Pt. I, p. 141). Some departures from homogeneity in age are inevitable in practice, but their effect is likely to be minimized if planting-machines are kept together, planting is started from a side or corner, and the planted area at all stages kept as compact as possible

In some groundnut units it is planned to use maize in the rotation, a crop which suffers severely from streak disease over much of Africa; but if fields are kept free from groundkeepers and grasses for some time before sowing, and small nearby patches of maize are prohibited, the only

likely source of infection for large units is the grass surrounding them. This menace of infection from the perimeter is, for the reasons which are our theme, likely to fall as the fields are made larger and more compact.

It is of interest that in the Middle-veld of the Transvaal, near Pretoria, attacks of streak disease so severe as to destroy the whole crop seem to be confined more or less to small fields and plots. Large fields do not suffer so severely; infection often reaches 100 per cent., but too late for a total loss of crop. One should, however, add that size of field is often a reflection of general farming practice, and the possibility of spurious correlation is not negligible.

These two examples relate to infection moving into fields. Provided that infection does not move far in considerable amounts, precisely the same arguments hold for infection moving out of fields. For example, there are two common virus diseases of beet in England, mosaic and 'yellows'. One of the chief ways in which infection survives the winter is in plants destined for seed production. Infection is picked up by the 'stecklings' in late summer, carried over the winter, and released from the seed-fields in spring. Consider this last point: the release of infection in spring. If the diseases are crowd diseases—mosaic almost certainly is, but the evidence about 'yellows' is still a little indefinite—then, on the same argument as before, the release of infection is favoured by the dispersion of the industry. At present the 8,000 acres under beet and mangold seed crops in Britain are divided among hundreds of large fields and thousands of small, and if the diseases are crowd diseases one of the first steps in national hygiene, distinct sometimes from local hygiene, would be to manipulate the seed contracts so as to encourage the large fields and discourage the small.

Size of field in relation to the eradication of sources of infection near the field.—So far we have considered just the automatic gains following concentration in large fields. Largeness of field, however, also helps positive efforts at sanitation. With crowd diseases it is commonly recommended that sources of infection near fields should be removed: alternate hosts of cucumber mosaic virus are removed from the immediate vicinity of susceptible crops, and two similar examples have been given above (pp. 142–3). The point to be remembered here is that the ease of maintaining a healthy belt around any given acreage under a crop depends on the size of the fields into which that acreage is divided (see Fig. 1, Pt. I, for the simple arithmetic involved). Whereas good sanitation may be very difficult near a large number of small fields, it is relatively easy and cheap around large compact fields. Largeness of field is in fact a usual prerequisite for good sanitation near fields.

Size of field in relation to infection carried by seed or sett.—The more easily infection can enter fields, the less is the need for the fields to be healthy at the start. With small, close fields, widely exposed to infection from without, emphasis must go on resistance to disease. The breeding for resistance to viruses of cassava for peasant cultivation in East Africa is an apt example. But large, distant fields, free from infected soil or groundkeepers, put a premium on healthy seed or setts. One might cite as an example the need for absolutely virus-free seed potatoes as a

commonplace product at reasonable prices for such fields; for such a product would stave off the necessity to replace seed-stocks for a number of generations that would depend on local circumstances.

Crowd diseases and systems of land usage.—Crowd diseases are favoured by any system that cuts up land into a large number of small fields and plots; and allotments, private gardens in towns and villages, and the small fields of peasant cultivation are examples of insanitary usage of land. Swollen shoot of cacao has marked characteristics of a crowd disease. According to a map published by Posnette [4] in 1947, the largest area of disease had reached only a radius of some 10 miles after spreading since about 1922, a slowness of spread remarkable even among crowd diseases; and the cacao industry is clearly a victim of peasant cultivation. As an alternative to the present costly measures of control, the idea might be pondered of a better system of land usage that would provide for a clean start, as opportunities occur, with large and compact blocks having all the isolation from one another that largeness and compactness can give. A possible complication now is that the virus may have invaded the indigenous vegetation, and that in reclaimed areas the problem may now be no longer just one of spread from cacao to cacao. This is a matter for local observation, but even if alternate hosts now exist, largeness of unit is still the first step in sanitation.

The point that, where crowd diseases are a menace, the needs of a plant health service should have an impact on political and administrative thought is too evident to warrant discussion here.

Discussion

In Part II [5] it was deduced from the available experimental evidence that making fields larger and correspondingly fewer would reduce the movement of air-borne fungus spores between them; also that in certain circumstances there is a fairly close horizon of infection from beyond which relatively little infection is received, even when the spores are able to travel great distances. It is therefore often possible considerably to reduce the amount of infection coming into a field by a process of enlargement; and in this respect there is no fundamental difference between crowd diseases and diseases caused by fungi with air-borne spores.

From this it might be argued that, if crowd diseases can be reduced by making fields larger and correspondingly fewer, similar reduction should be possible when the infection is air-borne fungus spores. But there is a fallacy here. Reducing the infection entering a healthy field is one thing, controlling the disease is another; for a control of disease does not necessarily follow a reduction of infection entering the field. When (to repeat for simplicity a much-quoted illustration) it is found that mosaic in a celery field can be controlled by destroying alternate hosts of the causal virus within 75 ft. of the field, the inferences are not only that this destruction greatly reduced the amount of virus reaching the field, but also that this reduction is useful in the control of the disease. Therefore, when one shows that making celery fields larger and correspondingly fewer would have an effect in the same direction as destroying alternate

hosts around the fields, one may legitimately argue that making fields larger and correspondingly fewer will also usefully control the disease. The second inference is implicit throughout our discussions of crowd diseases. It is believed to be correct, for reasons to be given shortly. But there are no grounds for a similar inference with most fungus diseases. The matter is one of methods of sanitation in general, rather than of enlargement of fields in particular, and as such it will be discussed.

What determines whether reducing the amount of infection reaching a healthy field will be useful in controlling the disease is the rate at which infection multiplies within the field. If, for example, infection takes a day to double itself, then halving the amount of infection reaching a field (by making fields larger and fewer, or by any other method of sanitation) will postpone the reaching of a severe level of disease by one day only, a result hardly worth striving for. But if infection needs a year to double itself, halving the amount of infection reaching the field will postpone the onset of serious disease by a full year—a much more desirable result. Of immediate interest is not just the reduction of primary sources of infection by sanitation, but also the period of time this gains in postponing a serious level of infection. Time is the crucial factor, because the time gained determines the crop gained; and arguing about sanitation as a means of gaining time, one may put as a general theorem that the value of any system of sanitation depends on the rate of multiplication of infection: the greater the rate, the less the value.[1]

With crowd diseases, by definition caused by infection that does not spread far in considerable amount, infection multiplies relatively slowly within a field. Therefore by the theorem just advanced, measures of sanitation are fairly effective; and if by making fields larger and correspondingly fewer one can reduce infection reaching a field, one can legitimately hope that this reduction will be useful in the control of the disease, especially with annual crops. But when infection travels far in considerable amount, as it often does with fungus diseases, it may also be expected to multiply rapidly within fields, and although making fields larger and correspondingly fewer can reduce the amount of infection reaching a field, the reduction may be of little use in the practical task of controlling the disease, even with annual crops. Exact correspondence between the distance over which infection travels and the rate at which it multiplies within a field requires that gradients of infection away from its source be of constant form. This assumption is an approximation. Usually differences between diseases caused by widely ranging fungus spores and crowd diseases are so great that variations in the form of the gradient are of minor importance. For example, *Puccinia graminis tritici* can move from Mexico to Canada in one summer; the swollen-shoot virus of cacao has taken some 25 years to move 10 miles. No differences in form of gradient are likely to alter significantly the expectation—borne out by observation—that the rust fungus can sweep through a field of wheat much more quickly than swollen-shoot virus does through

[1] To be precise, the rate here concerned is that just before the onset of serious disease, not the average for the season. For example, with potato blight in epidemic form it is the fast rate during the favourable weather that brings on the epidemic.

cacao. As another example, 100 years ago *Phytophthora infestans* spread across Europe with devastating speed, from which, whatever the form of the gradient, we infer that the susceptibility of the potato was great, so great that, as contemporary accounts show, fields of potatoes seemed to collapse within a week or even overnight [6].

That with crowd diseases the rate of multiplication of infection within a field is in fact slow enough for the control of disease by sanitation we infer from the experience that these diseases can be controlled by isolation (cf. Pt. I). From a theorem discussed in Pt. I, we can relate ability to control a disease easily by isolation with ability to control it by making fields larger and correspondingly fewer. Both methods of control require the same condition: that the reduced amount of infection which reaches the field should not multiply so rapidly that the reduction in infection is not worth while, the word rapidly having a relative meaning and differing according as the crops are annual or perennial. But with most diseases caused by air-borne fungus spores, isolation (except by very great distances) has proved of little value, and we infer that infection mostly multiplies too rapidly for the control of disease by the methods we are discussing.

These are the grounds for assuming that with crowd diseases, but not fungus diseases caused by widely spreading spores, making fields larger and correspondingly fewer can be a useful help in control.

To look at the matter from a rather different angle: diseases become less severe when, for example, the climate becomes less favourable for infection, or host-resistance is increased. The process can presumably be carried to a stage at which the multiplication of infection is slow enough for the method of enlargement of fields to be applied. But will it be worth while? If infection spreads slowly, there is a likelihood of severe disease only when each infection causes considerable loss, that is, when the lesions are very large or the disease systemic. The second alternative is the more important, and it is with systemic diseases that the method is most likely to be useful. These systemic diseases include not only virus diseases but a few fungus diseases like loose smut of wheat. It is not implied that every systemic disease can be controlled by this method—tobacco mosaic, for example, is an exception (cf. Pt. I), but it is implied that the method is probably unsuitable when infection causes small local lesions, as do many leaf-spotting fungi. For then, if the disease is severe enough to justify an attempt to control it by this method, infection is likely to multiply too fast for the method to work; and if infection multiplies slowly enough for the method to work, the disease is not likely to be severe enough to justify the use of the method.

The two conclusions are much the same, because the important crowd diseases are mostly systemic diseases. It would be too remote from our subject to discuss this connexion in detail. Let it suffice to point out that ability for infection to spread smoothly within a plant, which is ability to infect systemically, often goes with inability for infection to survive for long outside the plant or to move quickly from plant to plant—disabilities that make a crowd disease.

Summary

In the large fields of the new African groundnut schemes, groundnuts are likely to be safer from rosette disease and maize from streak disease than in small fields in the same regions. The discouragement of small seed-fields should help against the aphis-borne virus diseases of beet. In succumbing to swollen-shoot virus, the West African cacao industry seems to be a victim of peasant agriculture.

It is a condition for a useful result from making fields larger and correspondingly fewer that the rate of multiplication of infection within the fields should not be fast. It is probably too fast with most of the economically important fungi causing local lesions by airborne infection, and the method is likely to be useful mainly against the movement into fields of infection causing systemic disease.

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LAND-UTILIZATION IN THE WET TROPICS

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WITH PLATES 6, 7

IN the super-humid tropics of the equatorial regions the effective rainfall exceeds 80 in. per annum; the incidence is seasonally variable but it is unusual for any month to be completely rainless. The high rainfall is associated with high temperatures, with comparatively small annual and daily ranges, and high atmospheric humidity.

The characteristic conditions may be modified by geographical location and by land configuration; they occur most widely in south-east Asia, in Equatorial Africa, in the South and Central American regions, in the Caribbean area, and in the Pacific. The climatic factors are responsible for the soil and vegetational conditions and determine the agricultural uses to which the land can be put.

As the rainfall exceeds the evaporation the soils are pedalfers; drainage is of great importance, and the soil-vegetation complex varies according as it is free or impeded. Where it is unimpeded, as in mountainous or undulating upland regions, the soils are usually heavily leached and poor in mineral plant-food. Their character is affected by the nature of the parent rock; geologically old rocks, especially sedimentary rocks, give soils poorer than those derived from recent volcanic intrusions, whilst basic rocks give richer soils than acidic rocks high in silica. Nevertheless, under the climatic and vegetational influences, soils of approximately similar type can be produced from widely differing materials.

The vegetational climax is tropical rain-forest with heavy production of organic matter, which breaks down rapidly, liberating carbon dioxide and facilitating decomposition of soil minerals. Most usually, weathering leads to the elimination of silica and the formation of siallitic soils and subsoils yellow to bright red in colour and markedly acid in reaction.

The concept of the soil catena formulated by G. Milne [1] and developed by C. G. T. Morison and his co-workers [2, 3] is probably of particular significance in the super-humid tropics. Eluvial conditions will probably extend farther down slopes and colluvial conditions be more restricted than under sub-humid conditions, and this will affect land-use, since markedly eluvial conditions are unfavourable to crop-growth. Fig. 1 (Pl. 6), taken in southern Malaya, illustrates how the growth of young rubber can diminish as one proceeds up a slope and conditions become progressively eluvial.

Where drainage is impeded conditions are different. Valley-bottoms, alluvial flood-plains of rivers, and coastal alluvial flats provide examples. Leaching is largely arrested, accumulations of finer material transported from higher regions giving closer-textured soils. The vegetational climax may be swamp forest or swampy reed-growth, in coastal regions it may be mangrove swamp. Conditions are often anaerobic, accumulations of peat occur in places, and decay of organic matter is slower. The soils

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show great variability; often in an undrained condition they are infertile and contain toxic ferrous compounds, and sometimes the existence of ferrous sulphide leads to the formation of free sulphuric acid. Very often they are black or bluish clays and in coastal regions they are frequently highly impregnated with salt. In an undrained condition they are of little value, but when reconditioned by drainage they may be of considerable fertility.

In regions where active volcanoes occur, as for example in Java, Central and South America, and some of the West Indian islands, the periodic deposition of volcanic ash may affect soil fertility, masking the leaching effect on upland soils and enhancing fertility on lowland areas.

Organic matter and nitrogen.—Under conditions of unimpeded drainage organic matter disappears with extreme rapidity, the high temperature and humidity favouring intense biological activity. In tropical rain-forests, notwithstanding that organic matter is constantly added to the soil in large quantities (Vageler [4] estimates the amount as approaching or even exceeding 100 tons per acre per annum), there is no accumulation of a deep surface-layer of humus, in fact it is doubtful whether humus, in the sense accepted in temperate climates, is formed at all.

Closely connected are organic matter and soil nitrogen. The soil gains nitrogen through the agency of leguminous plants, and usually through the activities of free-living nitrogen-fixing bacteria (strains of azotobacter tolerant of the high acidity of the soils of the humid tropics have been shown to exist in Malayan soils by Altson), but their exact importance is still unsettled. Soils lose nitrogen through absorption by living plants, leaching, and denitrification. Owing to leaching there is no accumulation of nitrates in the surface-layers of the soil as occurs during dry weather in the sub-humid tropics. Wilshaw [5] has shown that under Malayan conditions great fluctuations occur in the soil nitrogen-content within short periods and the position is highly dynamic.

The carbon/nitrogen ratio is also important; carbon supplies energy for soil organisms and a correct balance in this regard is essential; if it falls too low the supply of nitrogen for growth is disturbed.

Under natural conditions in tropical rain-forest the soil-vegetation complex is a balanced system forming a closed cycle. Mineral plant-food is brought from deeper levels by the roots of trees and incorporated in the surface-layers through the fall of plant-remains. The carbon/nitrogen ratio is also maintained in a balanced condition, whilst erosion losses are held in check by the natural vegetational cover. So long as the cycle is maintained unbroken the position is stable, the vegetational cover retains its exuberant character, which, incidentally, is responsible for the long-sustained but erroneous belief in the wellnigh inexhaustible character of the fertility of the soils of these regions. Actually the balance is one of extreme delicacy and when it is interrupted by clearing and cultivation deterioration sets in unless measures are taken to prevent it. Organic matter rapidly disappears and the carbon/nitrogen balance is upset, the mineral plant-food elements concentrated in the surface-layer become depleted, and erosion losses of great magnitude occur.

Obviously land-utilization should be directed to preserving so far as

possible conditions approximating to those which obtain in nature, and this limits the uses to which they can be put.

Low-lying regions have a wider range of potentialities owing to their greater reserves of mineral fertility, better status in regard to organic matter, and reduced liability to erosion. The natural factors at work are similar to those in upland regions and agriculture must be directed towards conserving resources; but the margin is wider and the range of uses correspondingly more extended. On balance they represent the greatest asset of the super-humid tropics.

Land-use in Upland Regions

The type of agriculture suited to these conditions is that of permanent crops such as rubber, coffee, tea, cocoa, and oil-palms. The point has been recognized by many authorities: Stockdale [6], writing with reference to Malaya, points out that orchard or tree crops offer greater possibilities than the cultivation of annual crops; Engledow [7], writing on land-use in the British Colonial Empire, has stressed the same point; F. J. Martin [8] called attention to it in regard to Sierra Leone and advocated the discouragement of the cultivation of annual crops on the uplands and the encouragement of swamp rice and other annual crops on the low-lying swampy lands, and this recommendation was adopted as the official agricultural policy of the Sierra Leone Government.

Permanent crops facilitate approximation to natural conditions, but even so special precautions require to be observed. The maintenance of the supply of organic matter is essential, equally so are soil-conservation measures immediately the forest-cover is removed. Formerly it was current practice to burn timber and brushwood immediately after clearing, thereby leaving the bare soil exposed to erosive influence, whilst the ash from the burn was liable to be washed or blown away. Recent practice, however, favours stacking the timber in lines and leaving it to decay under natural influences, thereby conserving organic matter and mineral plant-food and providing some protection from erosion.

Specific mechanical conservation measures must also be provided such as storm drains, terraces, bunds, and silt-pits; on steeply sloping lands bench-terracing is usually essential. Combined with these must be provision of protective vegetational covers either as planted cover-crops or the selective weeding of natural vegetation. Formerly clean-weeding was the general rule on tea and rubber plantations in the Far East; much damage ensued, which has only of comparatively late years been checked by the use of more rational methods. Protective covers serve the double purpose of checking erosion and helping to maintain the soil organic matter.

In establishing permanent crops on sloping land, moreover, higher parts of slopes should be avoided, since the conditions are markedly eluvial; they are better left under the natural forest cover to provide additional protection against erosion. The natural acidity of the soils also affects the choice of crops grown, as their tolerance of acidity varies; tea and oil-palms, for example, are much more tolerant of acid conditions than is cocoa.

The surface-layer of newly cleared forest-land is usually sufficiently rich to enable the establishment of permanent crops without manure. With many crops, sustained yields at a low level can be maintained for long periods without manure, depending on the demands of the crop itself and on the nature of the parent rock from which the soil is derived. Hardy [9] has pointed out that in Trinidad the longevity of cocoa can be greatly influenced by this fact. As cropping proceeds the benefit from appropriate manurial applications increases. When permanent crops are removed as a prelude to replanting it is often necessary to manure before the new stand can be established. Haines [10] has stated, in relation to rubber in Malaya, that the deterioration in this regard can be diagnosed simply as nitrogen deficiency, whilst phosphate deficiency is also often a factor.

The cultivation of annual crops is severely restricted owing to conditions; shifting cultivation is extensively practised on small-holdings by native cultivators, the chenas of Ceylon and the ladangs of Malaya and Sumatra are examples. If the interval between successive cultivations are long enough, and particularly when only small trees and undergrowth are removed, natural regeneration can restore fertility, but if it is unduly shortened, or the attempt made to grow annual crops continuously without heavy manuring, the land deteriorates rapidly and is usually abandoned after a few years. The situation may be worsened by the invasion of cleared areas by the grass lallang (*Imperata cylindrica*) which, particularly because of its liability to be fired during dry spells, prevents the re-establishment of the natural vegetational succession. This has occurred over large tracts in Malaya as a sequel to attempts to cultivate cassava and pineapples as a main crop, and also in parts of Sierra Leone following the continuous cultivation of upland rice.

Cases exist of lands cleared for annual crops and kept clean-weeded becoming unproductive. J. Lambourne [11] records that at the Serdang Experimental Station in Malaya a quartzite-clay soil reclaimed from jungle and drained, after continuous cultivation under cassava with clean-weeding for five years, would not grow maize, tobacco, and similar short-term crops at all. When, however, dressings of pen manure or organic materials in the form of dried grass were given, normal growth was resumed, but artificials alone gave no response (see Figs. 2, 3, and 4, Plates 6, 7). Possibly readily attackable organic matter had been so reduced that it did not suffice to provide energy for the normal biological soil processes; incidentally, the soil contained much free carbon. By contrast in sub-humid climates continuous clean-weeding does not show this effect and may be productive of benefit. Presumably the humid conditions account for the difference.

Chinese market-gardeners in Malaya convert infertile mining tailings into fertile soil by the liberal use of organic material, including cut grass, sweet-potato vines, pig manure, and household refuse. Birkinshaw [12] also showed that it is possible by the use of organic material to recondition lands on which slimes from tin-dredging had been spread to a depth of several feet.

It seems that under super-humid conditions organic matter can play

an important part in maintaining soil fertility. Opinion is divided on the general role of organic matter in tropical soils, and the super-humid tropics may provide a key to the problem, since there the check or reversal of natural processes due to the long dry seasons of the sub-humid tropics is lacking.

Within limits, uses other than for orchard crops can be developed on upland soils. Intercalary food and cash crops are often grown between the rows of orchard crops during the early stages of development, taking advantage of the transient fertility and enabling some cash return to be obtained without impairing greatly the growth of the main crop. In this way many thousands of acres were established in rubber by Chinese planters, the crops grown including cassava, pineapples, and gambier.

Market-gardening for the production of vegetables can also be successfully practised: ample supplies of organic manures are needed which may have to be supplemented by artificials, and on sloping lands bench-terracing is essential. It can be successfully combined with dairying, poultry-keeping, and pig-raising. Costs are usually high and readily accessible markets capable of paying remunerative prices are essential.

The scope for animal husbandry is restricted; grazing is largely precluded owing to the high cost of establishing pastures, which will not in any case stand up to more than very light grazing, and the only practicable possibility is stall-feeding on cut fodder and purchased foodstuffs on the soiling system. Dairying on these lines has been developed to a limited extent in many countries, e.g. in Java, Malaya, and Ceylon. Supplies of green fodder are often difficult, many tall-growing fodder grasses grow well, e.g. Guinea Grass (*Panicum maximum*) and Napier fodder (*Pennisetum purpureum*), but with successive cuttings yields fall off unless they are manured. In many countries animal disease is also a difficulty, particularly tsetse-borne trypanosomiasis. Attempts to overcome this by keeping animals in fly-proof byres have met with some success in Nigeria and the Gold Coast. Costs are necessarily high, and animal husbandry to be successful depends on available markets, although possibilities exist for its combination with the cultivation of permanent crops on a limited scale primarily for domestic use but also for sale.

Wet rice is extensively grown on lower colluvial slopes in Eastern countries. The land is terraced and the crop planted in small bunded compartments, the soil being puddled to retain water on the land. The method favours accumulation of material from the upper slopes and leaching is largely prevented, thereby no doubt helping to conserve fertility.

Land-use on Illuvial Lands

Taken as a whole the low-lying illuvial lands of the super-humid tropics have a much more extended range of uses. Their character varies enormously and they frequently require considerable expenditure of money and effort before they can be used for cultivation, but they are often of relatively high fertility and allow of the permanent cultivation of a wide range of annual crops as well as many of the orchard crops which can also be grown on the uplands.

On this account their potential value for the production of food crops is great, in particular they provide conditions pre-eminently suited for wet rice. The alluvial flood-plains of the great rivers and the coastal flats of the Eastern tropics bear the rice crops upon which their dense populations depend, and there is little doubt that opening up of the vast undeveloped tracts of similar lands in other parts of the Wet Tropics could make important additions to the world's supplies of food.

Wet rice is mainly grown by peasant cultivators on small-holdings using hand-labour or primitive implements; its cultivation is laborious, exacting, and unpleasant. The extension of the cultivation is bound to be slow by these means and mechanization is the obvious alternative. Mechanical cultivation of rice has been developed in Carolina and Louisiana in the southern U.S.A., in Australia, and to some extent in the Piedmont plain of northern Italy, but its adoption in the wet tropics presents problems some of which are not yet completely solved, although efforts to do so are in progress in a number of countries and the possibilities are under examination in others.

An essential need is complete and effective control over the water-supply, including protection from flooding and the means for keeping water on the land for so long as it is needed for the growth of the crop and of removing it efficiently and quickly at the ripening stage and in preparation for the harvest. Drainage takes precedence of irrigation and frequently good crops of wet rice can be grown on rainfall alone provided the water is kept on the land. Irrigation is of value to make good seasonal variations in the rainfall, and commonly conditions permit of the development of irrigation projects.[1]

Other annual food crops can also be grown on lands of this type provided they are drained, such as dry grains including maize, a variety of pulses, some root-crops, and green vegetables. Where drainage is effectively controlled, wet rice can be grown in alternation with dry crops in succeeding periods. In the Preanger plain in West Java it is common to see rice in all stages of growth and on adjoining lands crops of dry grains or green vegetables. In parts of Malaya green-vegetable crops are often grown between two crops of rice.

A number of cash crops can also be grown, sugar-cane is well suited to such conditions provided drainage is adequate and the manurial requirements met. In British and Dutch Guiana the major part of the cultivated coastal alluvial lands are devoted to growing sugar-cane and rice. In West Java in former years sugar-cane, rice, and pulses were combined into a standard rotation, and there seems no prima-facie agricultural reason why such rotations should not be adopted under similar conditions elsewhere.

The perennial crops also do well, rubber, coffee, oil-palms, and even tea and cocoa thrive provided drainage is adequate and the soil acidity is suited to the needs of the crops. Coconuts, although they are for the most part grown on sandy soils with a moving water-table not far below the surface, are extensively grown on coastal alluvial clay lands on

[1] In some countries two or even three crops of rice are grown on the same land every year, using short-term varieties of the crop.

the western side of the Malay Peninsula when the lands are properly drained.

In view of their potential value for the cultivation of food crops it seems doubtfully wise policy to encourage the growth of permanent crops for export on lands of this type unless the foreseeable requirements for food-supplies are adequately provided for. In Malaya, for example, many thousands of acres of good potential rice-land were alienated for rubber cultivation. The Malayan Rice Cultivation Committee of 1931 recommended that, in view of the probable future requirements for rice of the growing population, no similar alienations should in future be made.

Once they have been reclaimed and drained, heavy alluvial lands often exhibit considerable reserves of fertility; for example, coconuts growing on such lands in Malaya gave no response to varying combinations of manurial applications. No doubt in due time, after prolonged cultivation, deficiencies would make themselves felt, but available evidence appears to point to such lands being cultivable for long periods in this crop before plant-food deficiencies show themselves. Numerous examples also exist of such lands continuing to give satisfactory rice crops for long periods without manure.

In British Guiana coastal alluvial lands, which, after long cultivation in sugar-cane, are deteriorating notwithstanding that they are manured regularly with sulphate of ammonia, benefit considerably from flood fallowing, i.e. submergence under water for periods of from 6 to 12 months or more. Similar beneficial results have been found to follow the practice on banana lands in Central America which had deteriorated badly from Panama disease. The reason for the improvement is not clear entirely, but the benefit is undoubted.

It seems possible that the regular submergence of the soil which is essential in the cultivation of wet rice may be equally beneficial, in which case the alternation of wet rice with dry crops may be an effective system of land-use.

As has been mentioned, the occurrence of tracts of peat of varying depth is not infrequent and their utilization presents a special problem. They are very acid and in an undrained condition are of little value; when they are drained they become fluffy and the organic matter disappears very rapidly with great shrinkage in volume. They can be used for certain crops: coffee does fairly well on the pegasse soils of British Guiana and also on the peat soils of Malaya, and recently there has been some development of pineapple cultivation on them in the latter country, whilst coconuts and oil-palms have also been grown on them. They grow fairly well in the early stages, but later as the peat-layer disappears the trees often lean badly and have to be propped, which is a disadvantage (Fig. 5, Pl. 7).

The alluvial lowlands offer greater scope for animal husbandry than the uplands, although the wet nature of the ground and liability to flooding limit the possibility of grazing, and livestock diseases are a difficulty. For large-scale grazing drainage is essential, but expensive drainage schemes for grazing alone are doubtfully economic. A period of resting under grass might be a useful component in a rotation for rice-lands; in

some tropical countries cattle actually are grazed on rice-lands between crops, whilst 2 or 3 years under grass forms part of the rotation on rice-lands in northern Italy, although conditions there are not comparable with those in the tropics.

Under very wet conditions water-buffaloes have advantages over cattle and may offer somewhat greater resistance to some of the maladies.

On the whole, however, the stall-feeding of livestock on the soiling system probably holds out the greatest prospects of success; supplies of green fodder are more easily provided, and the cultivation of grains and pulses facilitates the provision of concentrates; the waste products of rice-milling can supply quantities of concentrated stock-food, whilst oil mills for the treatment of copra, for example, can give supplies of press-cake.

Summary and Conclusion

The super-humid tropics present special problems of land-use; the heavy and continuous rainfall, high humidity, and high temperature produce the typical conditions that differ markedly from those of sub-humid regions, with heavily leached soils and rapid disappearance of organic matter when drainage is unimpeded; when drainage is impeded leaching is restrained, mineral fertility is higher, and organic matter accumulates; the soils are heavier and in their natural condition often unusable, but when reclaimed by drainage they may be of great value and have a wider range of uses than upland soils.

On uplands, permanent orchard crops are the most suitable form of cultivation as they permit the nearest approximation to natural conditions although limited possibilities in other directions exist. In alluvial lowland areas, although orchard crops may grow well, annual crops can be grown; in particular rice is well suited to such conditions, other annual crops can also be grown, and there is some scope for animal husbandry. On this account these regions are specially important from the point of view of food-supply.

Correct land-use is essential in view of growing populations and demands for food, and on this account the limitations imposed on land-use as a consequence of conditions must be recognized.

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FIG. 1. Young rubber on sloping land in Johore, Malaya, showing varying growth with fertility gradient on slope.

FIG. 2. Unproductive soil at Serdang, Malaya. Planted in maize without manure.

FIG. 3. Same soil as in Fig. 2. Planted with maize and dressed with complete fertilizer.

FIG. 4. Same soil as in Fig. 2. Planted with maize and dressed with farmyard manure.

FIG. 5. Coconuts on peat.

Pl. 7

PASTURE IMPROVEMENT IN NEW ZEALAND

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HIGH grassland production in New Zealand is due primarily to a climate eminently suited to grass growth. In the greater part of the country the range of temperature between summer and winter is not extreme, the rainfall is adequate and fairly uniformly distributed throughout the seasons, and the number of sunshine-hours per year is high. There are, however, distinct differences in climate between the North and South Islands, and within these general climatic regions local variations occur. Consequent upon these climatic differences there have developed different farming systems. In general, the regions of high rainfall and relatively small extremes between summer and winter temperatures are devoted to permanent pasture grassland farming of high production, whilst in the regions of lower rainfall and greater extremes in temperature arable farming with temporary or short-rotation pastures is practised, or permanent grassland comprised of low-producing species is maintained. The differences in climate between North and South Islands have been well set out by E. Bruce Levy in his book entitled *Grasslands of New Zealand*.

Climate has influenced not only the farming practices adopted in the various climatic regions but has also, over the years, profoundly affected exotic species of grasses and clovers imported into the country, and distinct ecotypes have developed. In those areas climatically suited to permanent grassland farming, persistent leafy strains have evolved, whilst under arable-farming conditions short-lived, stemmy, free-seeding strains have developed. Following the work of Levy and Davies [1] on the identification and classification of these ecotypes, a government certification scheme was inaugurated and the persistent ecotypes of the best permanent grasslands have been certified; but the short-lived types characteristic of arable farming areas have been rejected from the certification scheme [2].

Breeding-work.—Following the identification and certification of these strains, they have been improved by breeding, and additional strains have been produced for use in short-rotation and temporary pastures. The aim has been to provide strains which, when correctly used in pasture mixtures or in special-purpose pastures, will enable high pasture production to be maintained throughout a large part of the year.

All the species in which improvement by breeding is being sought are cross-fertilized and the genetic variability is so great as to provide ground for appreciable improvement by selection. Improvement in such features as yield, seasonal spread of production, and persistency, has frequently been accomplished by selection for these characters after accumulating a wide range of plant material. Genotype selection from an array of plants selected primarily on phenotype is based on progenies

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obtained by some form of open- or inter-pollination rather than on selfing with its consequent reduction in vigour. A progeny-testing technique based on open-pollination of plants in an 'increase area' (an area planted with spaced seedlings of an improved strain and harvested to provide a nucleus seed-supply) has been widely used to determine the breeding potentialities of plants to be used for strain building [3]. This test provides information similar to that obtained from crossing the plants to be tested to three common plants and has the advantage of simplicity. After the survey of the plant material by this preliminary progeny test, improved strains are produced, perhaps by the immediate combination of tested plants, or ultimately by the combination of further progeny plants obtained by intercrossing or inbreeding.

Hybridization has been used as a means of providing greater genetic variability for selection and to combine desirable characteristics from different strains and even species. For example, short-rotation ryegrass has been produced by selection from derivatives of hybrids between perennial and Italian ryegrass. Following hybridization between these two species and in some cases back-crossing to one or other of the parental species and then repeated maternal line selection, a strain of ryegrass has been produced that possesses desirable features of both perennial and Italian ryegrass and is stable for these characteristics.

All bred strains produced by this Institute are finally released into farming practice through the usual commercial channels under the control of government seed-certification, a system which ensures that the farmer obtains a standard product free from major contamination.

The exploitation of the potentialities of bred strains for high pasture-production necessitates an appreciation of the characteristics of these strains. Their efficient use is dependent on such factors as seasonal production, persistency, and their reaction to the grazing animal, particularly in so far as different types of grazing affect their vigour and competition one with the other in the mixed pasture. The chief characteristics of strains bred at the Grasslands Institute will therefore be considered in this paper as well as the bearing of these characteristics on the utilization of pedigree strains for increasing pasture production.

The genus Lolium contains species and strains of such diverse seasonal growth that it offers wide scope for breeding a range of strains to produce at almost all seasons of the year and for use in temporary, short-rotation, long-rotation, and permanent pastures. Pedigree strains have been produced of the following ryegrasses: perennial, Italian, short-rotation, and Western Wolths.

Perennial ryegrass (*L. perenne*).—Of the 'English' grasses imported into New Zealand by the early immigrants, probably the most valuable to the grassland economy of the country is perennial ryegrass. It is the basic grass for all high-producing permanent pasture seeds-mixtures in New Zealand. In the century that has elapsed since its importation, and by virtue of its use under widely divergent farming systems, a number of distinct ecotypes have developed. Under a system of permanent grassland farming in regions of ample and well-distributed rainfall favourable to high production, a leafy, vigorous, perennial strain has

evolved, whilst under a temporary or short-rotation system of farming in districts of lower rainfall short-lived strains have arisen. These have gradually eventuated from the practice of sowing a mixture of perennial and Italian ryegrass and harvesting for a seed-crop in the first season. From hybridization between the ryegrass species, sowing these mixtures, harvesting in the first season, and the repetition of this practice, a short-lived, free-seeding strain of ryegrass has evolved—a type which possesses the good characteristics of neither perennial nor Italian ryegrass.

In the breeding of perennial ryegrass, selection has been made from the perennial ecotype, and emphasis has been applied to increased leaf-production and persistency together with resistance to leaf-rust (*Puccinia coronata*), which often severely attacks ryegrass in late summer when there is little growth.

The seasonal production of pedigree perennial ryegrass compared with the best 'old pasture' strains of North Island and South Island origin is shown in Table 1. The ryegrass strains were sown at the rate of 40 lb. ryegrass and 3 lb. pedigree white clover per acre in 1/10-acre paddocks on April 10, 1947, and rotationally grazed by sheep. The production in dry matter per acre of ryegrass only to Nov. 30, 1948, is shown in the table.

TABLE 1. *Seasonal Production of Perennial Ryegrass Strains at Palmerston North*

In lb. dry matter per acre of ryegrass, from 6/6/47 to 20/11/48

Strain	*Winter*	*Spring*	*Summer*	*Autumn*	*Winter*	*Spring*	*Total*
Poverty Bay 'Old Pasture' . .	880	2,966	4,373	2,905	1,248	3,643	16,015
Pedigree . .	868	3,530	3,613	2,967	1,932	4,095	17,005
South Island 'Old Pasture' . .	559	4,304	2,299	1,310	1,068	3,061	12,601

The South Island strain, which has developed in an arable region, is higher producing than the pedigree strain in the first spring after sowing, but is much lower in the summer and autumn, and owing to poor persistency its subsequent production is low. It can, therefore, neither compete with pedigree perennial ryegrass for use in permanent pastures nor with Italian and short-rotation ryegrass for temporary or short-duration pastures. The production from the North Island Poverty Bay 'old pasture' strain is similar to that of the pedigree strain in the first year, but after the first autumn is appreciably lower, probably because of its rather poorer persistency. The relative persistency and susceptibility to leaf-rust of these three strains is shown by the figures from a trial where observations on individual plants were recorded at Palmerston North in the 1947/8 season (Table 2). The superiority of the pedigree strain in regard to resistance to leaf-rust is evident.

Where climatic and edaphic factors are suitable for maximum grass-growth, perennial ryegrass together with pedigree white clover is capable of very high annual production. At this Station, in pasture trials where

TABLE 2. *Persistency and Leaf-rust Susceptibility of Pedigree Perennial Ryegrass in Comparison with 'Old Pasture' Strains*

Strain	*Plants with leaf-rust per cent.*	*Plants surviving per cent.*
Best 'Old Pasture' North Island	41	76
Best 'Old Pasture' South Island	71	44
Pedigree	4	88

there is no limitation in available plant nutrients and fertility is maintained by a high stock-concentration on the pastures, yields of 14,000 lb. dry matter per acre per year have been obtained from pastures of pedigree perennial ryegrass and pedigree white clover, of which the average composition is approximately 70 per cent. ryegrass.

In comparison with many other permanent-pasture grasses, perennial ryegrass has a long seasonal spread of production. In the winter, however, its yield is much lower than that of the shorter-lived ryegrasses. At Palmerston North its winter production is usually about 25 per cent. of its maximum spring production, whilst the relative figure for short-rotation ryegrass is approximately 50 per cent. At Lincoln in the South Island where the winter temperatures are lower, the winter production of perennial ryegrass is on the average only 10 per cent. of its spring production, but that of short-rotation ryegrass is 30 per cent. This relatively low winter production of the perennial ryegrass/white-clover permanent pasture can in practice be largely remedied by including a proportion of short-rotation ryegrass in the pasture mixture.

A factor tending to limit the supply of seed and increase the seed-price of pedigree perennial ryegrass is its susceptibility to blind-seed disease (*Phialea temulenta*), which in seasons favourable to the disease drastically reduces germination. Attempts are now being made to breed a strain of perennial ryegrass resistant to the disease. Resistance has been shown to be inherited, but the resistant plants located are inferior agronomically to plants of the pedigree strain [4]. By repeated back-crossing of resistant plants to susceptible plants of pedigree origin further resistant plants have been obtained that are appreciably better agronomically than the original resistant plants. It remains to be seen, however, whether a good strain that is true-breeding for resistance and will maintain this resistance in the field can be obtained.

Italian ryegrass (*L. multiflorum*).—Italian ryegrass is an annual or biennial plant which has a much higher winter production than perennial ryegrass, although its growth in late summer and autumn is considerably lower. In the breeding of the pedigree strain of Italian ryegrass emphasis has been placed on high winter production, but at the same time the potentiality to persist into the second season has been increased.

To compare the production and ability to persist into the second year of the pedigree strain of Italian ryegrass with a standard strain of non-pedigree origin, a pasture-measurement trial was sown at Palmerston North in April 1947, in small replicated plots. These were sown with

ryegrass at 40 lb. per acre together with pedigree broad red clover at 4 lb. per acre, and production was measured by the Sears proportional technique [5]. The seasonal yields in lb. dry matter per acre are shown in Table 3. In the first year the total production of the two strains is very similar but the production (as ryegrass) of the pedigree strain is 16 per cent. greater than that of the certified commercial strain. It is in the second winter that the superiority of the pedigree strain is really shown when both ryegrass and total dry matter of the pedigree strain are greater, the former by 182 per cent. and the latter by 29 per cent. Of the total dry matter produced in the second winter it is significant that in the certified commercial strain 28 per cent. is produced by useless 'volunteer' *Poa annua*, which contributes only 7 per cent. towards the production of the plots sown with the pedigree strain. It is evident that the pedigree strain of Italian ryegrass is not only more productive than the certified commercial strain in the first year, but is decidedly more persistent and productive in the second winter.

TABLE 3. *Seasonal Production of Italian Ryegrass Strains at Palmerston North*

In lb. total dry matter per acre and ryegrass dry matter per acre, from 1/6/47 to 31/5/48

Strain	*Dry matter*	*Winter*	*Spring*	*Summer*	*Autumn*	*Winter*	*Total*
Pedigree .	Total	2,480	3,325	2,320	1,396	2,151	11,672
	Ryegrass	2,405	2,846	714	330	1,511	7,806
Certified Commercial .	Total	2,179	3,509	2,380	1,312	1,663	11,043
	Ryegrass	1,991	2,888	460	73	535	5,947

This greater persistency of the pedigree strain is also indicated by survival-counts made on the same two strains planted in the field in replicated blocks of individual plants. The percentage of plants surviving in the second year was 83 for the pedigree strain and 5 for the standard strain of non-pedigree origin.

The chief use of Italian ryegrass is for temporary pastures of one or two years' duration. When sown with red clover as a special-purpose temporary pasture, the Italian ryegrass produces during the winter, spring, and early summer; the red clover production is obtained in the late summer and autumn. The biennial nature of the pedigree strain of Italian ryegrass makes it a good counterpart to red clover for a two-year pasture as it persists sufficiently well to provide some grazing in the winter and early spring of the second year when red clover is practically dormant.

Short-rotation ryegrass (*L. perenne* × *L. multiflorum derivative*).—Short-rotation ryegrass was bred from hybrids between perennial and Italian ryegrass. By continued selection in derivatives of these hybrids for the growth-characteristics of Italian together with the persistency of perennial ryegrass, a strain of short-rotation ryegrass has been evolved that combines to a satisfactory degree the good qualities of both species, e.g. rapid establishment, winter production, and palatability (from

Italian), and density and persistency (from perennial ryegrass). It has a similar seasonal productivity to Italian ryegrass—its winter and early spring growth is slightly lower than that of Italian but about double that of perennial ryegrass. Production in late summer and autumn is superior to Italian but inferior to perennial ryegrass for this period. Table 4, based on a pasture-measurement trial at Palmerston North [6], indicates the seasonal production of short-rotation ryegrass in comparison with pedigree perennial and Italian ryegrass in the first 18 months after autumn sowing. The figures refer to the dry-matter production of ryegrass only in a ryegrass/white-clover pasture.

TABLE 4. *Perennial, Italian, and Short-rotation Ryegrass Production*

In lb. dry matter per acre of ryegrass

Species	*Winter**	*Spring*	*Summer*	*Autumn*	*Winter*
Perennial ryegrass . . .	369	2,283	2,150	1,774	853
Short-rotation ryegrass . .	953	2,881	2,450	1,374	1,545
Italian ryegrass . . .	1,206	2,984	1,766	515	1,074

* 2 months only.

A comparison between short-rotation and perennial ryegrass in regard to their seasonal productivity under comparatively high and low rainfall conditions is given by the results of pasture trials carried out at Marton in the North Island and Lincoln in the South Island. At Marton the average annual rainfall is 38 in., which is fairly evenly distributed throughout the year, whilst that at Lincoln is only 25 in., and less reliably distributed, particularly in the autumn. The average annual mean temperatures are lower at Lincoln than at Marton. In Tables 5 and 6 are shown the average production for a 4-year period of perennial and short-rotation ryegrass sown in trials at Marton and Lincoln respectively. In both trials the ryegrasses were sown at 40 lb. per acre together with pedigree white clover at 3 lb. per acre; at Lincoln 4 lb. per acre of pedigree Montgomeryshire clover was also included in the seeds-mixture. In each Table the total dry-matter production per acre is given as well as the production from ryegrass only. In both trials the significant difference between the two ryegrasses is the superiority of short-rotation ryegrass in the winter months. In both trials, too, it is rather less productive in the autumn.

TABLE 5. *Average Seasonal Yields of Perennial and Short-rotation Ryegrass*

In lb. total dry matter and ryegrass dry matter per acre for four years at Marton

Strain	*Dry matter*	*Spring*	*Summer*	*Autumn*	*Winter*	*Annual*
Perennial . .	Total	3,920	2,630	1,984	1,030	9,564
	Ryegrass	2,880	1,644	1,616	836	6,976
Short-rotation . .	Total	3,668	2,530	1,915	1,767	9,880
	Ryegrass	2,786	1,796	1,380	1,481	7,443

TABLE 6. *Average Seasonal Yields of Perennial and Short-rotation Ryegrass*

In lb. total dry matter and ryegrass dry matter per acre for four years at Lincoln

Strain	*Dry matter*	*Spring*	*Summer*	*Autumn*	*Winter*	*Annual*
Perennial . .	Total	1,753	1,298	470	159	3,680
	Ryegrass	1,356	600	354	140	2,450
Short-rotation . .	Total	1,895	1,197	398	487	3,977
	Ryegrass	1,563	620	262	453	2,898

Temperature and rainfall in the two districts have a profound effect on both annual and seasonal production. The annual production at Lincoln is less than half that at Marton. Approximately half the annual production at Lincoln is obtained in the spring. In this district the winter production of short-rotation ryegrass is equal to approximately 30 per cent. of its spring production, but for perennial ryegrass it is only 10 per cent. At Marton, where winter temperatures are higher, a greater proportion of the annual production is obtained in the winter with both perennial and short-rotation ryegrass, but the latter is still decidedly superior at this season. Stated as a percentage of the spring production, short-rotation ryegrass produces more than 50 per cent. in the winter, perennial ryegrass less than 30 per cent.

In persistency short-rotation ryegrass is intermediate between perennial and Italian. Its potentiality for high production and its relative persistency are largely influenced by grazing management; under continuous hard grazing it may be little better than an annual, but under *a lenient system of grazing combined with high soil fertility* it approximates to a perennial.

The main contribution that short-rotation ryegrass can make to increased pasture production arises from its ability to produce in the winter and early spring months when other permanent pasture species are producing but little. It is used as the basis of a special-purpose pasture of short duration or as a constituent of permanent pasture. In the former case it is sown with white clover and red clover to provide feed at those seasons of the year when permanent pastures are low-producing. The yield from the short-rotation ryegrass is high in the winter; in the late summer and autumn the clovers take up the role of production. If leniently grazed and 'spelled' at the correct time such special-purpose pastures can go a long way towards providing feed at these two critical seasons.

When used in a permanent pasture together with such species as perennial ryegrass, cocksfoot, white clover, and red clover, its early growth serves to extend the productive period of the pasture, and to increase the palatability of the pasture, particularly in the early stages before the clovers have become well established. The benefit of the short-rotation ryegrass will, however, not be fully realized if the pasture is continuously hard-grazed. Under such treatment it is liable to be 'eaten out' and dominated by the perennial ryegrass and white clover, which can tolerate harder grazing.

Western Wolths ryegrass.—Western Wolths is an annual variety of Italian ryegrass characterized by greater winter production than any other ryegrass. In the past, lines of true Western Wolths ryegrass have been imported into New Zealand mainly from Holland, but because the strain crossed freely in the field with perennial and Italian ryegrass its identity has been lost. A survey of lines harvested in New Zealand as Western Wolths ryegrass has revealed that less than 1 per cent. of such lines could be classified as predominantly Western Wolths ryegrass.

A pedigree strain of Western Wolths ryegrass has recently been produced at this Station but has not yet been increased for distribution through the seed-certification system. The objective has been to produce a strain which when autumn sown will establish rapidly and will provide a greater bulk of feed than will Italian ryegrass in the first 6 months after sowing. Its use would be to provide green feed in the winter and early spring when production from permanent grassland is relatively low. At the present time Italian ryegrass and various cereals such as barley, oats, and ryecorn are used for this purpose. Most of the cereals provide earlier feed than the Italian ryegrass, but they do not maintain their production through to the early spring as well. To be of value the pedigree strain of Western Wolths will need to surpass Italian ryegrass in the early period after sowing and maintain at least as high production through to the spring. An indication of its early production compared with that of pedigree Italian ryegrass is provided by figures from a production trial now being carried out at Palmerston North. In the first 4 months after sowing in the early autumn, plots sown with Western Wolths ryegrass have produced 1,856 lb. dry matter per acre compared with 1,488 lb. from the Italian ryegrass, a superiority in this period of 25 per cent. Further trials with this strain will be made in different climatic regions in comparison with Italian ryegrass and various cereals, and if it proves sufficiently superior to Italian in early production and to the cereals in sustained production the strain will be increased for distribution into farming practice.

Cocksfoot (*Dactylis glomerata*).—Where rainfall is lower and not so reliably distributed and where soil fertility is insufficiently high to favour high production from perennial ryegrass and white clover, cocksfoot is more suited to take up the role of the dominant permanent pasture grass. As a component of a permanent pasture along with perennial ryegrass, cocksfoot has the valuable attribute of maintaining its production during the autumn period if the available moisture is too low for growth of perennial ryegrass. But where conditions favour perennial ryegrass it will suppress cocksfoot, which is slower to establish and under severe grazing less vigorous in growth. The main objectives, therefore, in breeding a pedigree strain of cocksfoot have been to increase its vigour of growth and its speed of establishment in an endeavour to produce a strain that is less likely to be suppressed in a mixed pasture by the vigorous ryegrasses.

The New Zealand Akaroa strain of cocksfoot has been shown by Levy and Davies [7] to be superior in vigour and persistency to various imported strains, and the plant material used at this Institute in breeding a pedigree strain was obtained mainly from lines of Akaroa cocksfoot.

The increase in vigour and production of the bred strain over the standard New Zealand strain is shown by the following figures obtained from pasture trials, carried out at Palmerston North and Lincoln. In both cases the cocksfoot was sown with Italian ryegrass and white clover. At Palmerston North over a 3-year period the pedigree strain produced 20,350 lb. dry matter of cocksfoot per acre compared with 17,184 lb. from the standard strain. At Lincoln, during a 2-year period, the yields have been 6,720 lb. and 4,722 lb. for the pedigree and standard strain respectively.

Timothy (*Phleum pratense*).—Timothy is used in most seeds-mixtures for permanent pasture, but except in Southland the acreage harvested for seed is small, and most of that sown in the past has been of seed imported from North America. Imported lines have marked limitations in leafiness and persistency. The seasonal production is short, for growth begins late in the spring and there is a long dormant period in the winter. From observations made on New Zealand harvested seed it appears that there have been no pronounced ecotypes developed in New Zealand as in the ryegrasses, cocksfoot, and white clover, although lines from Southland are more leafy and flower slightly later than imported American strains. The study of a large array of strains from America and Europe has shown that the Welsh Plant Breeding Station 'pasture hay' and 'hay' strains, S48 and S51, are superior in this country to all other imported or New Zealand strains in leafiness, production, and winter-greenness. The superiority is so outstanding that these strains have been used to provide the basic plant material for a strain produced at this Institute. The relative production and persistency of this strain compared with an American imported line are shown by the data from a pasture trial sown at Palmerston North on October 1, 1945. The timothy was sown in a mixture with Italian ryegrass and white clover. Over a 3-year period the total production of the pasture sown with the pedigree timothy was 34,224 lb. dry matter per acre, whilst that of the pasture sown with the imported timothy was 29,516 lb. Moreover, the yield of timothy itself was 16,234 lb. for the pedigree compared with 8,578 for the imported strain. At the end of the 3-year period the percentage of timothy in the pasture sown with the pedigree strain was 55, as against only 34 per cent. in the pasture sown with the imported line.

White clover (*Trifolium repens*).—White clover in New Zealand has provided a wide field for selection, for there are extreme differences between strains and individual plants in such characters as productivity and longevity. In their investigations on white clover Davies and Levy [8] identified strains ranging from a small-leaved, non-vigorous, practically annual type to a vigorous, high-producing, persistent type, which they designated Type 1. Following this work the white-clover certification scheme was inaugurated to identify and certify areas producing this type, which incidentally embraced only about 5 per cent. of the white clover harvested for seed at that time. Bred lines based on this Type 1 ecotype and selected for greater vigour, persistency, and extended seasonal growth have been produced and are certified. The relative production of this pedigree strain compared with the best certified New Zealand strain of non-pedigree origin and with an ordinary

uncertified New Zealand strain is shown by the data in Table 7 from a trial carried out by Gorman [9] at Palmerston North. The trial was sown in Nov. 1945 in replicated plots with a seeds-mixture of pedigree ryegrass at 40 lb. per acre and white clover at 3 lb. per acre, and measured by mowing without grazing. The yields to Aug. 1948 for total dry matter per acre and for clover dry matter per acre shown in Table 7, together with the percentage of clover present in the latest cut, indicate the relative productivity and persistency of the various clover strains under competition from the ryegrass.

TABLE 7. *White Clover Strains*

Dry-matter production from November 1945 to August 1948 at Palmerston North

Strain	*Total D.M. lb. per acre*	*Clover D.M. lb. per acre*	*Per cent. clover at latest cut*
Uncertified N.Z. . .	21,672	10,041	14
Certified non-pedigree .	25,717	15,421	29
Pedigree . . .	27,166	17,676	53

White clover is used in all seeds-mixtures for short-rotation and permanent pastures and is undoubtedly the species which contributes most to the thrift and high production of the best grasslands of New Zealand, not only from its own contribution to that production but also from its effect on the yield of the associated grasses in the pasture. In all pastures nitrogen is essential to grass-growth, and in the high-producing pastures of this country it is the white clover that maintains the nitrogen status of the pasture. The effect of the pedigree strain of white clover in increasing the production of associated grasses has been demonstrated by Levy and Sears [10] at this Station. A mixture of potentially high-producing grasses sown without white clover has yielded approximately 4,000 lb. dry matter per acre annually, whilst the production from the same grass mixture sown with pedigree white clover was approximately 13,000 lb. The association of this white clover has increased the production of the grasses themselves from 4,000 lb. to 8,000 lb., quite apart from the extra production from the white clover itself amounting to 5,000 lb. per acre. It was shown that pedigree New Zealand white clover growing under the best conditions produced by itself as a pure sward approximately 10,000 lb. dry matter per acre with a total nitrogen-fixation equivalent to approximately 2,000 lb. of sulphate of ammonia per acre per annum.

The ryegrass/white-clover combination is the pasture *par excellence* for climatic and edaphic conditions where the summer and autumn are not too severe. However, in regions where the summer drought extends so far that autumn merges sharply into winter, production from white clover is low and greater reliance is placed on red clover.

Red clover (*Trifolium pratense*).—Two varieties of red clover are used in pastures in New Zealand: broad red clover which may be classified on the basis of its annual production as a double-cut variety, and Montgomeryshire red clover which is essentially a single-cut red clover.

The Montgomeryshire strain was introduced into New Zealand only about 20 years ago, and since its introduction it has been certified as a distinct strain that has been used for short-rotation and permanent pastures particularly in the South Island. It is essentially a summer- and autumn-growing variety and particularly in the lower rainfall areas of the South Island produces well when the yield of white clover is low.

A pedigree strain of Montgomeryshire red clover is now certified that is rather more vigorous and uniform to type but still retains the growth characteristics of the imported strain.

New Zealand cowgrass or broad red clover is earlier flowering, has a lower leaf-stem ratio, begins growth earlier in the spring, and is less persistent under grazing than Montgomeryshire red clover. In the pedigree strain, improvement in leafiness, production, and persistency has been effected. The data in Table 8 on the production of the pedigree strain compared with the commercial strain of broad red clover and with pedigree Montgomeryshire red clover were obtained at Palmerston North and Lincoln. In both districts the trials consisted of replicated plots of pure sowings of red clover, and in each case measurements by mowing were made for a period of 20 months.

TABLE 8. *Red Clover Strains*

Dry-matter production for 20-month period at Lincoln and Palmerston North

Strain	*Palmerston North D.M. lb. per acre*	*Lincoln D.M. lb. per acre*
Commercial Broad . .	12,154	8,686
Pedigree Broad . .	13,882	10,292
Pedigree Montgomery .	11,990	10,465

In each district the production of the pedigree strain of broad red clover is greater than that of the commercial strain, although the difference is not large—6 per cent. at Lincoln and 14 per cent. at Palmerston North. Broad red clover and Montgomeryshire red clover are very similar in total production, but the former has a rather longer seasonal spread of production, commencing growth earlier in the spring.

The Utilization of Pedigree Strains of Pasture Plants to Increase Production

The productive potentialities of the pedigree strains of pasture plants produced at this Station having been briefly discussed, it is proposed to consider the methods of utilizing these strains so that the most can be made of their potentialities. Their most efficient use in pastures depends largely on their growth-characteristics, and particularly on their seasonal growth. To obtain maximum production throughout the year attention must be given to the best combination of strains and species in a seeds-mixture and to the most appropriate management of the resulting pasture to ensure the maximum productivity of each species consistent, of course, with high nutritive value.

The two periods of low pasture-production in New Zealand are the

winter and later summer, and if these gaps can be bridged by the use of selected grasses and clovers that grow during these periods, then higher production per acre should be realized. In many parts of New Zealand, particularly in the North Island, very little cropping is undertaken and the stock are dependent almost solely on pasture. Under such a farming system the periods of low grassland-production can be alleviated either by conserving excess pasture production in the form of hay and silage or by the use of special-purpose pastures to provide feed during these months.

The conservation of excess pasture-growth in the form of hay and silage is a common practice and a reliable insurance against periods of pasture shortage. Where low winter production from permanent pasture sets the limit to the stock-carrying capacity of the farm, and a high peak of growth is obtained in the late spring and early summer, it is sound practice to conserve this surplus growth as hay or silage to supplement the winter food-supply and to control rank pasture-growth. Nevertheless, it is a wasteful method, for as Sears and Goodall [11] have shown, there is a loss under normally good conditions of between 30 and 40 per cent. of dry matter in the process of converting pasture into silage, and under farming conditions the losses are considerably greater.

To obtain a seasonal spread of pasture production in conformity with stock requirements advantage can be taken of the different seasonal-growth characteristics of the various pasture species and strains. For instance, the seasonal spread of production of a permanent pasture consisting predominantly of perennial ryegrass and white clover can be extended by including in the seeds-mixture short-rotation ryegrass and Montgomeryshire red clover, the former to increase the winter production and the latter the late summer production. But as different strains and species demand different grazing management for their maximum production, their full potentialities cannot be easily obtained when they are used as constituents of a complex mixed pasture. To make full use of their out-of-season production they should be used as the basis of relatively simple special-purpose pastures. For instance, a temporary pasture sown with Italian ryegrass and broad red clover can be managed so as to give high winter production from the Italian ryegrass and a good bulk of late summer feed from the red clover.

The ability of Western Wolths, Italian, and short-rotation ryegrass to produce in the winter months can be exploited by using them as the basis of temporary or short-rotation special-purpose pastures. Of these three ryegrasses the annual Western Wolths is the highest winter producer and is used alone or with a winter-growing cereal as a temporary pasture to produce winter green-feed. Where a 2-year pasture is required primarily to give winter and later summer feed Italian ryegrass sown with broad red clover can be used, the Italian ryegrass producing the winter feed and the red clover growing in the late summer when the ryegrass is non-productive. Under favourable conditions the pedigree strain of Italian ryegrass will persist sufficiently well after the first summer to give a good bulk of feed in the following winter, and in the second summer its place will be taken by the red clover. Where special-purpose

pastures of longer duration are required short-rotation and perennial ryegrass together with white clover and red clover should be used. Such a pasture if leniently grazed has a long seasonal production with the main contribution in the winter coming from the short-rotation ryegrass and in the late summer from the red clover. During the period when these two species are not growing rapidly, production is maintained by the perennial ryegrass and white clover, a very highly producing combination in the spring, summer, and autumn months.

From this outline of the breeding of strains of pasture species in New Zealand it will be realized that the prime objective in the plant-improvement programme has been to obtain increase in production and in the seasonal spread of that production. The climate over most of the country is favourable to high and sustained grassland production; the strains have been produced which are inherently capable of this production, but their potentialities will be completely expressed only when those environmental factors under the control of the farmer are so moulded as to suit their particular characteristics. Sound farming practice that will maintain soil fertility and intelligent grazing management are fundamental pre-requisites to the full exploitation of the inherent potentialities of bred strains of pasture species. With full attention given to these factors in the use of pedigree strains soil fertility is conserved and a higher and sustained level of production can be maintained throughout the year.

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THE B-VITAMINS IN GRASS

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THE view now commonly held, that ruminants are independent of exogenous sources of B-vitamins, is of long standing, and originated in the work of Theiler, Green, and Viljoen [1], Bechdel [2], and others. McElroy and Goss [3] have since provided quantitative evidence of synthesis in the rumen, and their findings have been confirmed by the work of Wegner, Booth, Elvehjem, and Hart [4, 5]. It is thus understandable that little attention has been given to the B-vitamins of pasture grass, and that the literature provides little information on this subject.

It should be noted that the diets fed by McElroy and Goss (loc. cit.) and by Wegner *et al.* [4] were partly artificial. Where natural diets have been fed, as by Wegner *et al.* [5], Hunt *et al.* [6, 7], Lardinois, Mills, Elvehjem, and Hart [8], evidence for the synthesis of certain of the B-vitamins was by no means conclusive. Not one of these workers was able to show, with any certainty, that on such diets the rumen-contents contained more thiamin than was supplied by the food ingested. The findings of Lardinois (loc. cit.) show that the synthesis of pantothenic acid and vitamin B_6 is at least doubtful, and that there is only a slight increase in riboflavin. On the other hand, Hunt (loc. cit.) has reported a substantial increase in the amount of riboflavin, and Wegner [5] in all the B-vitamins investigated other than thiamin. It cannot, therefore, be taken for granted that all members of the B-complex are invariably synthesized by ruminants on a natural diet, indeed it would appear doubtful whether thiamin is ever produced under such circumstances. Thus, any assumption that the amounts of the B-vitamins in the diet of ruminants are of no importance may be premature.

It should not be forgotten that there are farm livestock other than ruminants which subsist in part and in certain cases wholly on grass, and which are able to synthesize vitamins of the B-complex in only small degree or not at all. Nicotinic acid is the only member which is known with certainty to be synthesized by the horse [9, 10]; in horses at grass and receiving no supplementary foods, deficiency of one or more of the B-vitamins would thus seem to be possible. Even horses on a hay and cereal diet may be receiving inadequate amounts of riboflavin. Carlstrom and Hjärre [11] in Sweden, and Jones, Maurer, and Roby [12] in the U.S.A. have reported suspected deficiencies of thiamin and riboflavin, respectively, in horses.

Pigs, e.g. breeding sows running out to grass, will usually receive supplementary rations of some kind, but there can be no assurance that these rations will contain adequate amounts of all the B-vitamins. Deficiencies of riboflavin and/or nicotinic acid would seem, under some circumstances, to be at least possible. This being so, the B-complex in the grass consumed would be of some moment.

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The requirements of poultry for riboflavin have been investigated by Bethke and Record [13], Bolton [14], Temperton [15], and others; there is no doubt that riboflavin deficiency occurs in poultry under practical conditions giving rise, in the case of chickens, to curled-toe paralysis, loss of weight, and nervous symptoms, and in breeding stock to decreased hatchability in the egg, smaller egg-yield, and loss of body-weight. Biotin deficiency would also seem to be a possibility when certain types of diet are fed to poultry under intensive conditions. Cravens, Almquist, Norris, Bethke, and Titus [16] have recommended that the biotin allowance for laying hens should be 0·154 μg./gm. of food fed. Certain foods frequently fed to poultry contain much less than this figure; for example, Lardinois *et al.* [17] have shown that maize and wheat contain 0·055–0·085 and 0·025–0·140 μg./gm. respectively. According to Lampen, Bahler, and Peterson [18], potatoes contain as little as 0·017 μg./gm. If grass can be shown to contain appreciable amounts of these two B-vitamins, then there is further good reason for the inclusion of dried-grass meals in all classes of poultry feeds.

Experimental

Materials.—An investigation of the B-complex of individual grassland species was considered fundamental, and material for this purpose was available in the Nursery at Cockle Park, where a large number of grasses, legumes, and herbs were under cultivation. These included most of the components of the old Clifton Park mixtures, in addition to some of those species most commonly found in modern leys.

The species studied, together with some relevant data, are shown in Table 1:

TABLE 1. *The Grasses Investigated*

Species	*Date of sampling*	*Flowering stage E = early P = pre- L = late*	*Method of drying*	*Thiamin*	*Riboflavin*	*Nicotinic acid*	*Pantothenic acid*	*Biotin*	*Pyridoxine*
				μg. per gm. dry matter					
Achillea millefolium (yarrow)	21.8.47	E	Oven	4·25	11·9	43·2	5·1	0·195	12·5
Plantago lanceolata (narrow-leaved plantain)	14.8.47	E	Air	4·07	10·5	38·4	5·6	0·254	13·2
Poterium sanguisorba (burnet)	28.8.47	E	Air	3·97	11·9	36·8	11·7	0·207	18·8
Cichorium intybus (chicory)	14.8.47	P	Air	3·11	13·6	57·5	18·8	0·242	13·4
Trifolium hybridum (alsike)	21.8.47	E	Air	2·99	12·1	27·7	22·1	0·389	14·1
Lotus corniculatus (trefoil)	28.8.47	E	Air	3·49	16·0	34·5	20·2	0·474	8·6
Medicago sativa (lucerne)	5.9.47	E	Oven	2·57	15·1	40·4	43·4	0·547	11·6
Onobrychis sativa (sainfoin)	28.8.47	P	Oven	2·46	16·3	47·3	15·4	0·471	10·7
Lolium perenne (perennial rye-grass)	28.8.47	P	Air	2·36	13·1	38·4	17·4	0·384	12·9
Phleum pratense (timothy)	14.8.47	L	Air	3·86	12·6	37·9	9·1	0·168	11·7
Dactylis glomerata (cocksfoot)	2.10.47	P	Oven	1·64	9·2	32·7	4·7	0·108	5·5
Poa trivialis (rough-stalked meadow grass)	28.8.47	E	Air	1·61	13·6	37·5	11·6	0·266	14·2
Cynosurus cristatus (crested dogstail)	28.8.47	P	Air	1·98	20·4	46·3	15·5	0·407	14·7
Festuca pratensis (meadow fescue)	28.8.47	P	Air	3·77	13·4	43·6	5·1	0·162	15·0
F. rubra subsp. *fallax* (Chewings fescue)	2.9.47	P	Air	4·36	17·5	34·9	15·5	0·238	14·8
F. elatior (tall fescue)	2.9.47	E	Oven	4·04	13·7	44·9	7·7	0·137	7·0
F. genuina rubra (red fescue)	2.9.47	P	Oven	2·82	12·8	42·9	12·3	0·118	12·2
Molinia coerulea (flying bent)	6.7.47	P	Oven	4·24	14·0	42·8	4·6	0·273	7·7
Eriophorum vaginatum (draw-moss)	20.5.47	L	Oven	3·01	12·4	44·0	7·4	0·227	11·9
Juncus squarrosus (stool bent)	25.6.47	E	Air	2·26	11·5	42·9	9·7	0·321	12·9

Sampling was carried out by means of sheep-shears, the plants being cut at approximately 1 in. above ground-level in order to minimize soil contamination. Care was taken to ensure that a representative sample was always obtained.

An effort was made to air-dry all samples in the absence of light, but some were affected by mould and had to be discarded, and these were replaced by samples which had been taken for another purpose and oven-dried. It was realized that drying at 60° C., the temperature employed, was likely to affect the amounts of thiamin and pantothenic acid found, and this has been taken into consideration in presenting the results. Samples were ground in a Christy-Norris mill using a $\frac{1}{32}$-in. sieve.

In addition to the examination of individual species from the Nursery, samples of mixed herbage were also obtained from the Palace Leas meadow hay plots in 1946 and 1947. In 1946 representative samples were taken from the swath on the day following mowing. The grass, when cut, was at an advanced hay-stage, some species being in the seed-head. Much rain had fallen immediately before sampling, and probably some losses of the vitamins had occurred by leaching.

In 1947 the same plots were sampled twice, once from the swath (June 27) immediately after cutting, and a second time from the pike (July 2). This season's crop was slightly less mature when cut than that of the previous year.

The numbers of the plots sampled, and the manurial treatments which they have received continuously since the experiment was begun in 1897, are set out in Table 2:

TABLE 2. *Manurial Treatments of Plots*

Plot	*Manures applied annually (per acre)*
1	8 tons dung, 37½ lb. sulphate of ammonia, 50 lb. nitrate of soda, 150 lb. basic slag, and 50 lb. muriate of potash
2	8 tons dung
6	Unmanured
7	150 lb. sulphate of ammonia
8	300 lb. basic slag
9	100 lb. muriate of potash
10	150 lb. sulphate of ammonia and 300 lb. basic slag
11	150 lb. sulphate of ammonia and 100 lb. muriate of potash
12	300 lb. basic slag and 100 lb. muriate of potash
13	150 lb. sulphate of ammonia, 300 lb. basic slag, and 100 lb. muriate of potash
14	75 lb. sulphate of ammonia, 100 lb. nitrate of soda, 300 lb. basic slag, and 100 lb. muriate of potash

Two-thirds of each sample was air-dried, and the remaining one-third oven-dried at 60° C. for 12 hours with a view to determining whether drying temperature had any effect on certain vitamins of the B-complex. Thereafter, treatment of samples was the same as that given to the species samples referred to above.

The following vitamins were determined on all samples from both

Nursery and Palace Leas: thiamin, riboflavin, nicotinic acid, pantothenic acid, biotin, and vitamin B_6. Tryptophane, which is known to be a precursor of nicotinic acid for certain of the farm animals, was estimated in the 1946 samples from Palace Leas.

Methods.—The possibility of employing chemical methods was considered, but it was found that, in certain cases, they were not suitable for the materials, and that in others the necessary apparatus was not available. Microbiological methods were therefore adopted, and proved, in general, to be satisfactory (Table 3).

TABLE 3. *Microbiological Methods of Assay*

	Method of assay	*Comments and modifications*
Thiamin	Sarrett and Cheldelin [19]	B_1-free grass extract added to basal medium
Riboflavin	Snell and Strong [20] as modified by Barton-Wright and Booth [21]	B_2-free grass extract added to basal medium
Nicotinic acid	Snell and Wright [22] as modified by Barton-Wright [23]	..
Pantothenic acid	Barton-Wright [24]	High recoveries were obtained unless an alkaline grass extract, freed from the vitamin by irradiation, was included in the basal medium
Biotin	Barton-Wright [24]	..
Vitamin B_6	Stokes *et al.* [25] as modified by Barton-Wright [24], and modified again by Tatum *et al.* [26]	The results obtained by methods [24] and [26] agreed very closely
Tryptophane	Greene and Black [27] as modified by Barton-Wright [28]	Ether and toluene extractions proved unnecessary for grass. Method of extraction may destroy some tryptophane

Results

In Table 4 are set out the amounts of the B-vitamins contained in the herbage (3.8.46 and 27.6.47) and hay samples (2.7.47) derived from the Palace Leas meadow hay plots.

It will be noted that the herbs, and certain of the poorer grasses (the fescues), are amongst the best sources of thiamin. One of the moorland species, viz. *Molinia coerulea*, has an equally good content of this vitamin. Of the cultivated grasses, only *Phleum pratense* is comparable with the foregoing.

Two of the poorer grasses (*Cynosurus cristatus* and *Festuca rubra* subsp. *fallax*) contain more riboflavin than any of the other species examined here, whilst *Dactylis glomerata* has less. As a group, the legumes would appear to be above the average.

Nicotinic-acid content shows comparatively slight variation as between

TABLE 4. *Vitamin-contents expressed as μg./gm. of Dry Matter, Tryptophane as Percentage of Dry Matter*

	Thiamin			*Riboflavin*			*Pantothenic acid*			*Nicotinic acid*			*Pyridoxine*			*Biotin*			*Trypto-phane*
Date of sampling:	3.8.46	27.6.47		2.7.47	3.8.46	27.6.47	2.7.47	3.8.46	27.6.47	2.7.47	3.8.46	27.6.47	2.7.47	3.8.46	27.6.47	2.7.47	3.8.46	27.6.47	2.7.47	3.8.46
Method of drying:	*Air*	*Oven*	*Air*	*Air*	*Air*	*Air*	*Air*	*Air*	*Oven*	*Air*	*Air*	*Air*	*Air*	*Air*	*Air*	*Air*	*Air*	*Air*	*Air*	*Air*
Plot 1	1·52	2·45	3·30	2·17	6·4	8·9	7·8	7·8	7·6	14·6	11·1	22·0	30·1	31·1	7·9	10·3	7·9	0·151	0·195	0·168	0·117
2	1·53	1·82	3·39	2·21	8·3	11·1	8·9	8·6	7·5	14·0	16·2	27·7	33·2	37·6	7·6	11·3	7·3	0·150	0·202	0·159	0·134
6	1·97	1·70	3·83	1·87	7·8	11·6	12·2	8·6	15·4	16·4	33·9	43·5	46·0	8·8	11·0	7·0	0·179	0·179	0·139	0·161
7	1·65	2·50	3·78	2·90	7·6	13·4	12·4	11·6	9·3	14·1	15·8	27·7	31·6	42·2	8·7	11·5	7·1	0·190	0·166	0·163	0·112
8	2·34	1·54	3·75	3·05	10·2	12·1	12·6	9·1	7·7	17·7	16·2	27·3	36·6	48·2	8·7	10·1	6·8	0·222	0·183	0·160	0·112
9	2·46	1·65	3·75	2·64	8·4	11·7	12·6	7·1	8·1	14·8	10·7	27·9	32·8	44·4	8·9	11·4	6·0	0·174	0·192	0·189	0·103
10	2·03	2·09	3·38	3·15	7·1	12·9	12·0	8·8	10·8	17·7	11·3	25·5	44·7	37·2	9·0	12·4	6·4	0·204	0·219	0·224	0·101
11	2·45	1·64	2·55	1·90	9·3	11·8	11·8	8·4	8·1	16·6	9·9	36·1	29·7	37·2	9·8	11·1	6·6	0·207	0·143	0·185	0·123
12	1·88	2·30	2·51	3·08	9·7	12·8	12·4	9·2	8·8	14·3	13·3	34·3	33·1	42·9	9·0	13·5	6·5	0·156	0·196	0·185	0·122
13	2·77	1·80	3·44	3·02	10·0	12·1	13·9	8·2	8·9	13·8	12·2	38·1	32·6	43·9	9·3	12·8	6·9	0·146	0·194	0·208	0·114
14	1·91	2·23	2·79	3·03	9·9	13·2	14·3	7·3	9·9	17·9	13·1	25·9	34·9	37·5	8·8	12·3	6·5	0·150	0·224	0·173	0·102
Mean .	2·05	1·97	3·31	2·94	8·61	11·96	11·90	8·61	8·66	15·54	13·29	29·67	34·80	40·75	8·59	11·61	6·82	0·175	0·190	0·177	0·118
Standard error	0·13	0·10	0·19	0·15	0·39	0·37	0·58	0·38	0·31	0·49	0·74	1·52	1·17	1·51	0·18	0·31	0·15	0·008	0·007	0·007	..

most species. *Cichorium intybus* is, however, a fairly good source and *Dactylis glomerata* a poor one.

The proportions of pantothenic acid present are very variable, but the legumes as a group are good, *Medicago sativa* being outstanding. The three moorland species contain little of this vitamin, as also does *Dactylis glomerata*.

The grasses and herbs in general contain variable amounts of biotin. *Lolium perenne* is, however, the best grass, and *Dactylis glomerata* the poorest of all species. The legumes were uniformly good sources.

There is considerable variation in vitamin B_6 and in this respect no particular group is clearly superior to another. *Poterium sanguisorba* contains more than any other individual species and *Dactylis glomerata* contains least.

The figures in Table 5 do not show any evidence of a relationship between manurial treatment and content of the B-vitamins; they do indeed suggest that manuring has been without appreciable effect, although the variation justifies only a tentative conclusion.

The effect of season on certain of the B-vitamins has been very marked, the differences between the mean contents of thiamin, riboflavin, pantothenic acid, and vitamin B_6 in 1946 and 1947 are very highly significant ($P = 0{\cdot}001$). Nicotinic acid also shows a significant difference, but biotin does not ($P = 0{\cdot}05$).

Losses of thiamin and pantothenic acid as a result of oven-drying have been very large, amounting to 40·5 per cent. and 44·3 per cent. respectively ($P = 0{\cdot}001$).

The actual curing process resulted in significant losses of thiamin, pantothenic acid ($P = 0{\cdot}05$), and pyridoxine ($P = 0{\cdot}001$). Riboflavin and biotin were not present in significantly different amounts from samples in the swath and pike. Nicotinic acid was alone in making a significant gain ($P = 0{\cdot}05$).

Discussion

The literature of the B-vitamins in respect to their occurrence in individual pasture species, or indeed in herbage younger than at hay-stage, is not considerable. The vitamin-B potency of lucerne has been most studied, presumably because it is frequently included in poultry feeds; particular attention has been paid to riboflavin-content. Hunt [29], using a biological method of assay, and working on lucerne, timothy, and smooth-stalked meadow grass, obtained values for riboflavin of 9–26 μg./gm. dry matter. Lucerne and timothy gave results which closely approximate to those obtained in the present investigation; in both instances the stage of maturity at sampling was almost the same. Hanke and Perkins [30] determined the riboflavin in a large number of lucerne samples by a fluorimetric method, and found a range (8·95–25·75 μg./gm.) which was virtually identical with that of Hunt (loc. cit.); artificial drying proved superior to sun-curing. Bauernfeind, Norris, and Heuser [31] have recorded the pantothenic-acid content of 4 samples of dehydrated lucerne which were found to have a range of 33·3–46·0 μg./gm. These figures are reasonably close to the single value for

the lucerne shown in Table 1. The relatively high content of this last sample is perhaps noteworthy because it was oven-dried; as already indicated, the authors have shown that oven-drying can result in losses of up to 44·3 per cent. of the pantothenic acid present. Hale *et al.* [32], using a chemical method, found 157 and 66 μg. nicotinic acid per gm. dry matter in clover and blue-grass respectively. Both of these values are higher than any obtained in the present investigation—the first of them markedly so. These apparent discrepancies may well be due to differences in maturity at sampling. Kohler [33] has shown that increasing maturity of the oat plant is accompanied by a marked and consistent decline of nicotinic-acid content.

The values for thiamin obtained from individual grassland species (Table 1) suggest that when stock graze the best modern leys they are unlikely to obtain very large amounts of this vitamin from the grasses; nor are clovers particularly good sources.[1] The tendency of such stock to eat any rough materials they may obtain in hedge sides or elsewhere has often been noted and commented on. The fact that some of the so-called herbs and certain of the poorer grasses appear to be particularly good sources of thiamin may afford a partial explanation of a habit which, to the ley-farming enthusiast, may savour of depravity. Swards derived from complex seeds-mixtures, e.g. mixtures of the Clifton Park type, should provide much larger amounts of thiamin to grazing stock, than do their modern counterparts.

As an appreciable proportion of artificially dried grass is used for inclusion in poultry feeds, and as such feeds tend to be deficient in riboflavin, the amount of this vitamin present in grass is important. Our results suggest that a ley which is to be cut for drying should contain a reasonable proportion of legumes, but that the grasses should not be entirely of those species which are conventionally regarded as 'good'. A useful clover-content is desirable on all grounds, but a superabundance of the better grasses, and more especially of cocksfoot, will not conduce to a higher riboflavin-content. When dried grass is fed to housed cattle, it is not likely to prove of much value as a source of the B-vitamins. When the ration contains oats, as it often will, there should be no question of thiamin deficiency.

The only considerable body of information relating to the vitamin-B complex in hay is due to Lardinois, Elvehjem, and Hart [17], who examined alfalfa, timothy, and clover hays in respect of thiamin, riboflavin, nicotinic acid, pantothenic acid, and biotin; also the effects of storage and grinding.

As the immediate effect of differing manurial treatment is on the balance of species present, and as it has already been shown that substantial differences in respect of the B-vitamins exist between species, it is logical to suppose that the amounts of these vitamins present in the herbage could be related to the manurial treatment. As already indicated, the results obtained fail to provide evidence of any such relationship.

[1] Data obtained by the authors, and as yet unpublished, show Kentish Wild White, Dutch White, and S.100 White clovers to have the relatively low thiamin-contents of 1·23, 0·60, and 2·35 μg./gm. dry matter respectively.

The very large differences between the amounts of B-vitamins present in the 1946 and 1947 crops can probably be ascribed entirely to the different weather of the two seasons. The fact that biotin, which is the least easily extractable member of the complex, provided the sole exception in not being present in significantly lesser amounts in 1946 points to losses of the other vitamins as being largely due to leaching. The summer of 1946 was conducive to such losses, whilst that of 1947 was exceptionally dry for NE. England. Another factor, although one which was probably of secondary consequence, was the state of maturity at cutting. The 1946 crop was cut 5 weeks later than that of 1947, and was somewhat more mature, although it should be emphasized that this difference in maturity bore no direct relationship to the interval between the cutting dates; if the hay-crop matured rather late in 1946, it matured exceptionally early in the droughty year of 1947. The adverse effect of increasing maturity on the B-vitamins has been demonstrated by Kohler [33] and by Hunt [29].

It was expected that thiamin, pantothenic acid, vitamin B_6, and riboflavin would suffer losses during the curing process as they are known to be unstable to light when in solution. The first three did, in fact, show a significant decline, but riboflavin was unaffected. For this latter result, as for the significant rise in nicotinic-acid content, the authors are unable to account. No part of such losses as occurred could be attributed to leaching, as no rain fell between cutting and piking.

It would appear that whatever beneficial effects may result from the application of fertilizers to the hay-crop, an increased content of the B-complex is not one of them. At the same time, there is no more satisfactory evidence that a reduction is likely to occur; the contention that vitamin-content is adversely affected by the use of artificial fertilizers therefore finds no support here, at least in so far as the B-vitamins are concerned. Weather probably constitutes the major factor in determining the vitamin-B content of meadow grass. Losses of certain of the B-vitamins in the curing process are substantial, and although it seems logical to assume that more efficient methods would reduce them, experimental proof is still wanting.

Summary

Samples of individual herbage species, and of meadow grass at two stages of curing, have been assayed for thiamin, riboflavin, nicotinic acid, pantothenic acid, biotin, and vitamin B_6. Microbiological methods were used.

Considerable differences in vitamin-content, especially of pantothenic acid and biotin, were shown to exist between species. The legumes as a group were superior, in most respects, to the grasses and herbs. The poorer grasses were not inferior to the better ones.

There were significant differences between the 1946 and 1947 hay-crops in their contents of thiamin, riboflavin, nicotinic acid, pantothenic acid, and vitamin B_6. Considerable losses of thiamin, pantothenic acid, and vitamin B_6 resulted from hay-making. There was no evidence that fertilizer treatment affected the vitamin-B content of hay.

The practical implications of these findings have been discussed.

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THE COMPOSITION OF TIMOTHY (*PHLEUM PRATENSE*) AND SOME OTHER GRASSES DURING SEASONAL GROWTH

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THE present lack of concentrated feeding-stuffs has emphasized the need for making the fullest use of our pastures and much work has been done on the effect of various types of management, application of fertilizers, and methods of grazing. Whether grass is to be grazed or conserved, a knowledge of its chemical composition at different stages of growth is important if the best use is to be made of the crop and if as much consideration is to be given to quality as to quantity. The early work of Fagan, Milton, and Provan [1] on the effect of time and frequency of cutting on the yield and composition of Italian ryegrass showed that as the plants matured the protein-content decreased rapidly and the amount of fibre increased. Despite such knowledge, much of the dried grass produced in recent years has been little better than very good hay and in places so diverse as Northern Ireland [2], the east of Scotland [3], and Norway [4] the average crude protein content of hay has been as low as 8, 6, and 6 per cent. and such figures are probably no worse than those for hay in many parts of the British Isles.

The present work was designed to determine the normal growth-curve of established timothy (*Phleum pratense*), a grass grown considerably in south-west Scotland for hay and more recently and to a lesser extent for pasture. At the same time a study was made of the changes taking place in the content of the major chemical constituents of the grass, and the opportunity was taken to compare the results with similar data obtained from several grasses in their first year of growth.

It is well known that after grass has grown to a state in which the protein-content is relatively low, the percentage of protein in the leaves, as distinct from the stems, may still be relatively high and the leaf-fibre content low. If grass of this type could be separated commercially into leaf and stem, it might be possible to obtain a protein concentrate suitable for milk production from what would otherwise be a very poor product. A secondary object of the present investigations was therefore to consider whether there was any evidence that fractionation of this type would be warranted.

Experimental

Grasses used.—Scotch timothy of the hay-pasture type was sown in 1945 on well-drained land, which was in good heart, with a pH of 5·8 and no deficiency of mineral elements. It was cut for hay in that year and again in 1946, when the aftermath was also taken. In the early spring of 1947 the grass was cut to a uniform height of 1–2 in., and from May until the end of July a representative sample was cut at weekly intervals. Three further cuts were taken during August and September.

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For comparison, in the spring of 1947, four hay grasses, Ayrshire perennial ryegrass (*Lolium perenne*), Danish cocksfoot (*Dactylis glomerata*), meadow fescue (*Festuca pratensis*), and Scotch timothy (*Phleum pratense*) were sown and samples taken periodically from each as soon as the plants had grown to an average height of 4–6 in.

Analyses.—The size of the sample varied somewhat with the stage of growth but usually about 1 kg. of grass was taken from representative plants; grass which had been cut once and had subsequently grown again was not included in the later cuts. Since carotene was to be estimated, precautions were taken to prevent losses due to light and tissue damage prior to the actual determination. For determining carotene, Booth's [5] method of pigment extraction with a mixture of acetone and light petroleum in the presence of an anti-oxidant was used and all samples were at the acetone-removal stage within 30–45 min. after cutting; the carotene was separated on activated alumina. Moisture and crude protein were determined on the whole fresh plants and again on the separated leaf and stem fractions. Although Gibbs [6] has shown that leaf-sheath lies intermediate in chemical composition between leaf and stem, no attempt was made to separate the sheaths as it was felt that the proportion by weight of sheath to either leaf or stem was at all times relatively small and the sheath was often difficult to distinguish with certainty. The ratio of leaf to stem on a dry basis was calculated from the respective fresh-weights and moisture-contents. If the grass had flowered, the flowering head was removed from the stems and analysed separately. Growth was assessed by measuring 100 plants and collecting the results into size groups at 4-in. intervals; the number of plants falling within each group gave approximately the percentage of the herbage at each size.

True protein, crude fibre, ether-extractives, and ash were determined at a later date on samples dried and ground to a fine powder on the day of cutting. True protein was estimated by the tannic-acid method of van Roth [7]. The procedure recommended by the Association of Agricultural Chemists [8] was not used since it was found that it was more likely to give erroneously high results with finely ground grass than van Roth's method. Particles of grass powder persistently floated on the surface of the liquid during the time of reaction with cuprous hydroxide without taking part in the reaction. These would be filtered off with the precipitate and estimated as true protein although still containing non-protein nitrogen. Crude fibre was determined by the single-solvent method of Whitehouse, Zarrow, and Shay [9]; comparison of this method with that of the A.O.A.C. [10] revealed no significant difference in the results, but showed that the method of Whitehouse *et al.* was much less troublesome and time-consuming.

Results

Established timothy.—Table 1 records the height of the established timothy from May to October, the ratio of leaf to stem on a dry-weight basis, and the moisture-contents of the whole plants and their constituent parts. There was continuous, rapid growth up to the end of June,

TABLE 1. *Growth of Established Timothy Grass*

Date (1947)	Length of plant (in.) % plants in each group									Ratio leaf to stem (dry wt.)	Moisture-content, %			
	<6	6–9	10–13	14–17	18–21	22–5	26–9	30–3	>33		Whole	Leaf	Stem	Head
May 20	32	59	9	..	..	..	..	..	..	2·57	77·2	76·6	83·8	..
26	15	52	28	5	..	..	..	..	..	2·15	81·6	78·1	83·1	..
June 2	..	16	27	23	23	11	..	..	..	1·30	79·0	78·4	84·2	..
10	..	..	23	41	30	6	..	..	..	0·58	80·6	77·3	81·6	..
16	..	..	10	29	47	14	..	..	..	0·39	76·1	78·0	72·9	78·2
23	..	..	..	12	46	26	11	5	..	0·41	72·2	72·7	71·4	71·4
30	..	..	..	17	21	21	23	18	..	0·35	65·5	68·5	63·1	60·5
July 7	..	..	..	..	9	26	43	18	4	0·21	65·2	66·9	63·7	65·2
14	..	..	..	4	15	27	37	15	2	0·20	65·0	66·5	60·4	63·6
21	..	..	..	..	..	19	37	33	11	0·16	68·2	72·0	60·5	68·5
Aug. 11	..	..	..	..	2	11	30	37	20	0·19	53·8	53·2	56·1	45·7
Sept. 3	..	..	..	..	4	21	29	34	12	0·16	44·8	20·8	49·5	17·8
25	..	..	..	..	14	22	14	27	23	0·18	46·3	23·8	50·5	..

TABLE 2. *Chemical Composition of Established Timothy during Growth*

Date (1947)	Crude protein (%)	True protein (%)	Carotene mg./kg.	Crude fibre* (%)	Ether-extractives* (%)	Ash (%)
May 20	18·4	16·5	274	20·3	3·54	8·00
26	18·8	15·7	273	23·2	3·56	8·50
June 2	14·2	12·8	156	26·3	3·74	7·15
10	10·6	8·8	128	28·7	2·91	7·72
16	9·2	8·7	108	30·8	3·02	6·86
23	7·1	5·8	74	32·6	2·18	6·50
30	6·3	5·5	72	30·4	2·12	5·98
July 7	6·8	4·4	66	31·2	1·79	6·12
14	5·5	3·8	88	32·1	1·64	5·62
21	4·2	3·0	44	32·3	1·42	5·32
Aug. 11	3·9	2·6	42	35·1	0·97	5·19
Sept. 3	2·5	2·2	33	34·7	0·97	4·41
25	1·9	1·7	9	39·6	0·73	6·01

* Calculated from leaf and stem data.

TABLE 3. *Chemical Composition of Timothy Leaf during Growth*

Date (1947)	Crude protein (%)	True protein (%)	Carotene mg./kg.	Crude fibre (%)	Ether-extractives (%)	Ash (%)	CaO (%)	P_2O_5 (%)
May 20	21·7	18·6	343	19·1	3·79	7·09	0·55	1·54
26	21·5	17·6	400	22·0	3·91	8·06	0·43	1·62
June 2	17·2	16·0	341	23·8	4·73	6·51	0·70	1·41
10	15·2	13·3	251	24·9	4·45	9·55	0·70	1·23
16	18·5	16·0	369	26·1	4·14	8·01	..	..
23	13·7	11·4	259	27·1	3·55	8·02	..	..
30	12·3	9·2	170	26·9	3·26	8·76	..	..
July 7	11·6	9·0	205	27·9	3·08	9·05	0·78	0·78
14	11·1	9·4	203	30·6	3·24	8·96	..	..
21	10·7	9·2	120	30·2	2·93	8·90	..	..
Aug. 11	8·7	6·6	64	31·8	2·69	9·31	..	..
Sept. 3	6·1	5·1	33	33·8	2·14	9·03	..	..
25	5·9	5·0	14	35·9	2·05	9·59	..	..

TABLE 4. *Chemical Composition of Timothy Stem during Growth*

Date (1947)	*Crude protein* (%)	*True protein* (%)	*Carotene* mg./kg.	*Crude fibre* (%)	*Ether-extractives* (%)	*Ash* (%)	*CaO* (%)	P_2O_5 (%)
May 20	14·1	11·1	86	23·5	2·87	9·95	0·20	2·15
26	14·1	11·5	112	25·9	2·77	9·46	..	..
June 2	11·4	8·6	61	29·7	2·46	7·95	0·23	0·89
10	7·4	6·1	45	30·7	2·03	7·37	0·18	0·83
16	7·6	5·9	71	32·6	2·56	6·65	..	..
23	4·8	3·5	32	34·9	1·62	5·91	0·14	0·89
30	4·4	4·2	32	31·7	1·72	5·01	..	..
July 7	3·4	3·3	35	31·9	1·52	5·59	0·14	0·93
14	3·4	2·7	48	32·4	1·32	4·96	0·14	0·71
21	1·9	2·0	23	32·7	1·18	4·76	0·13	0·60
Aug. 11	2·2	1·8	34	35·7	0·64	4·35	..	..
Sept. 3	2·3	1·7	14	34·9	0·78	3·66	..	..
25	1·8	1·6	12	40·2	0·49	4·71	..	..

after which the rate was slower and less uniform. Flower-heads emerged between June 10 and 16 and shed their seed towards the end of August. Although this was not predominantly a hay grass the proportion of leaf to stem quickly fell to a roughly constant value of about 1 : 5 by early July. The increase in dry matter was not appreciable until most of the grass was taller than 18 in., and only in August and September, when most of the leaves and stems were brown and woody, had the moisture-content fallen below 50 per cent.

Table 2 gives the chemical composition of the whole plant calculated on the weight of dry material, Table 3 similar data for the leaf fraction, and Table 4 analyses of the stems. Only crude protein and carotene were determined in the flower-heads and both constituents remained fairly constant at 12·5 per cent. protein and 70 mg./kg. carotene from June to seed-shedding in late August.

These tables show that at all times of the year timothy leaf contained appreciably more protein, more ether-extractable material, more carotene, and less fibre than the stem or whole plant. The ash-content (including silica) fell slightly in the whole plant and in the stem as maturity advanced, but in the leaves, which constituted a decreasing proportion of the ageing plant, there appeared to be a slight increase. The amount of calcium in the ash of the leaf rose slightly during advancing development whilst the phosphorus-content fell correspondingly, whereas in the stem both constituents decreased from the time of first cutting. These trends agree with those recorded by Fagan *et al.* for Italian ryegrass. Irregularities in the general trend of carotene values in the stem material can be attributed to the difficulty of extracting small amounts of pigment from woody material.

Table 5 gives the correlation coefficients between protein and carotene, protein and fibre, and protein and ether-extractives. With 11 degrees of freedom they are all highly significant at the 0·001 level, that between protein and fibre being negative.

First-year grasses.—Of the four first-year grasses, timothy, cocksfoot, fescue, and ryegrass, most data were collected from the timothy, and

TABLE 5. *Correlation of Protein with Carotene and Fibre*

	Correlation coefficient		
	Whole plant	*Leaf*	*Stem*
Protein with carotene . .	0·97	0·89	0·94
,, ,, fibre . . .	−0·90	−0·96	−0·86
,, ,, ether-extractives .	0·87	0·84	0·92

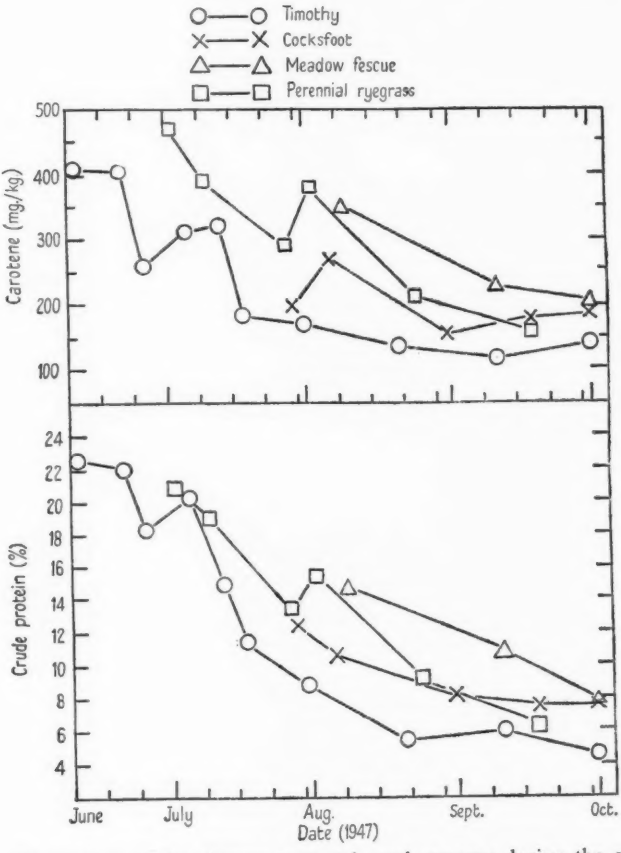


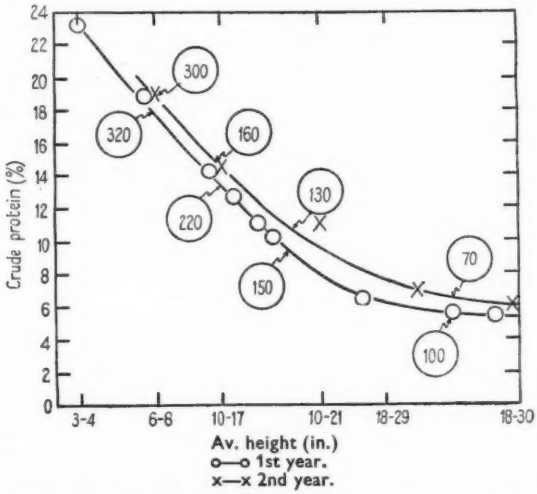
FIG. 1. Comparison of the changes in protein and carotene during the growth of some first-year grasses.

since the chemical composition of the other three grasses varied more because of differences in their rates of establishment than because of species, it will be sufficient to give the data for the first-year timothy in detail (Table 6) and a graphical representation, Fig. 1, of the protein and

carotene contents of the other three. Chemical analyses were confined to moisture, crude protein, and carotene in these grasses.

TABLE 6. *Composition of Timothy during First Year of Growth*

Date	Average height (in.)	Moisture-content (%)	Ratio leaf : stem (dry wt.)	Crude protein (%)				Carotene (mg./kg.)			
				Whole	Leaf	Stem	Head	Whole	Leaf	Stem	Head
June 12	3–4	80·9	Mainly leaf	22·6	..	..	..	408	..	..	..
20	4–6	83·4	4·50	22·0	23·6	13·8	..	405	484	91	..
26	7	80·9	3·22	18·4	21·2	16·4	..	259	379	100	..
July 4	8	81·8	2·40	20·3	21·8	13·6	..	312	484	110	..
11	14	82·8	1·11	14·9	18·6	8·1	15·9	323	388	115	127
17	15	75·0	0·98	11·5	16·4	5·5	13·6	183	283	52	96
30	18	73·5	0·60	8·9	15·9	4·5	13·3	170	312	46	103
Aug. 20	22	61·0	0·40	5·5	10·8	2·9	12·5	138	277	56	64
Sept. 10	22	70·5	0·52	6·0	12·8	2·8	13·0	117	202	35	95
30	24	59·7	0·41	4·6	8·8	2·4	..	141	201	43	..



The encircled numerals indicate the carotene-content in mg./kg.

FIG. 2. A comparison of first- and second-year timothy grass at the same stage of growth.

Compared with the established timothy, the grasses in their first year possessed more protein and carotene when compared on a chronological basis, but if compared at approximately the same height, as in Fig. 2, although small differences do exist, it is doubtful whether these are significant.

The four young grasses followed much the same pattern in protein and carotene composition (Fig. 1) although the meadow fescue was considerably slower in becoming established. This agrees with general experience that fescue is a somewhat difficult grass to establish.

Discussion

Probably the most important change shown in the foregoing data is that relating to the decreasing ratio of leaf to stem as the grass matured. As soon as the first leaves had produced sufficient material for the formation and emergence of a flower-head, the stem rapidly elongated without commensurate production of leaf, and the proportion of leaf to stem fell quickly. It can be seen that since the leaf possessed more protein, more carotene, more ether-extractable material, and less fibre than the stem, and over a considerable period had a higher mineral-content, as soon as the stem began to preponderate the content of more useful constituents decreased sharply. This is of utmost importance, whether the grass is to be grazed or conserved. Watson [11] has recently reviewed the literature bearing on the nutritive value of silage and dried grass, and all the data show that much greater differences exist in the chemical composition of a given grass at different stages of its growth than between such diverse grasses as cocksfoot, Yorkshire Fog (*Holcus Lanatus*), and bent (*Agrostis* spp.). More than 20 years ago Fagan [12] and his colleagues at Aberystwyth emphasized the different contribution which the leaf and stem fractions make to the composition of the whole plant, and later work on many grasses and legumes [13, 14, 15, 16] has confirmed the existence of similar relationships. The present work on timothy also shows that the stage of development, governing as it does the leaf-stem ratio, governs in turn the chemical composition of the whole plant.

The high carotene value in the early growth, particularly in the leaf (as seen in the above data for both young and established timothy) has been noted in other grasses and in legumes [17, 18]. As shown in Table 5, a high correlation between carotene and crude protein in the freshly cut grass existed in the whole plant and in both leaf and stem. Julèn [19], dealing with timothy cut at intervals between May and July, also found a high correlation between these constituents ($r = 0{\cdot}92$), but a lower negative correlation ($-0{\cdot}49$) between crude protein and fibre. Moon [13], analysing a mixed sward at intervals during the year, correlated protein and fibre with carotene and obtained coefficients of $+0{\cdot}89$ and $-0{\cdot}88$ respectively.

Although the nutritive value of herbage can best be assessed by animal experiments, chemical composition is undoubtedly a useful guide [20, 4]. Thus Drapala, Raymond, and Crampton [21] have shown that there is a marked increase of undigested tissue with increasing maturity of the forage. From Tables 1 and 2 it would appear that a predominantly timothy herbage grown for conservation, particularly by drying, should not exceed 9–12 in. in height and should be mown for hay at 20–4 in. Any increase in bulk after the grass has reached these heights will be unlikely to compensate for the loss in nutritive value.

Turning to the problem of whether it would be profitable commercially to separate leaf from stem in grass which had grown past the optimum cutting time, it is reasonable to assume that this would be justified only when the leaf portion contained at least 5 per cent. more

crude protein than the whole plant. From the data in Tables 2, 3, and 6 it appears that these conditions prevailed over a 10-week period (June 17–August 25) for the established timothy and over a 12-week period (July 20–September 30) for the first-year growth. In addition to the difference in protein between leaf and whole plant, however, the actual protein level of the leaf must also be considered, since leaf fraction containing less than 18 per cent. crude protein could not be considered a concentrate substitute. This second condition reduces both periods to 2 weeks. These grasses had not received any nitrogenous fertilizers in the year under consideration and it is known that heavy dressings can considerably increase the crude protein-content [22]. Such dressings also often encourage early leafiness [1, 23], so that the effect of such applications would be to extend the period of usefulness of leaf-stem separation. A small machine has been built in these laboratories which effects a satisfactory separation of the leaf of legumes, but in grasses the mechanical difficulties of completely separating leaf from either leaf-sheath or stem are considerable. It therefore appears most unlikely from the data so far available that the extra capital cost involved in separating a leaf-fraction from grass, assuming a machine could be made, would be justified in view of the successful efforts now being made to breed late-maturing grasses [24]. It may be noted that the pneumatic type of grass drier, such as the Swedish 'Pehrson' [25], does effect a type of leaf-stem separation by virtue of the quicker drying of the chopped leaf fragments, and it would be interesting to learn whether this type of machine could be adapted to produce a differentiated product from stemmy grass of which the leaf still contained a high percentage of protein.

Summary

1. The composition of the herbage on an established pure timothy sward was studied during one growing-season. The ratio of leaf to stem fell sharply with advancing maturity and this was reflected in a similar decrease of protein, carotene, and ether-extractable material, with a corresponding increase in crude fibre. The leaf fraction at all times possessed less fibre and more of the other constituents analysed. Highly significant correlation coefficients were found between crude protein and carotene, crude protein and fibre (negative), and crude protein and ether-extractable material in the whole cut and also in the leaf and stem fractions.

2. Similar studies on the composition of timothy in its first year of growth showed that when compared with the established grass on a height, as opposed to a chronological basis, the differences in protein and carotene contents were small.

3. Allowing for the different rates of establishment in the first year of growth, a comparison of the protein and carotene contents of timothy, meadow fescue, perennial ryegrass, and cocksfoot in plants at the same stage of growth showed only very small differences.

4. The feasibility of utilizing the higher protein-content of the leaf of grass that has grown past the optimum stage for conservation by separation of the leaf from the stem was considered. With grasses producing

maximum protein-contents of the order of 18–20 per cent. (dry wt.), the process would not be justified because of the short time over which even the leaf portion could be classed as a concentrate. It appears doubtful on the evidence available whether, even with heavy applications of nitrogenous fertilizers to increase protein-content and leafiness, the process would be economically worth while.

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THE APPLICATION OF MODIFIED PROCEDURES IN DIGESTIBILITY STUDIES

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Introduction

THE technique of conducting digestibility experiments with animals, which has been fully described by Watson and Horton [1], depends upon obtaining samples of faeces that correspond exactly with the quantity of food consumed. The conventional procedure consists in carefully weighing the amounts of food eaten and of faeces excreted for a fixed period of time, after a suitable pre-collection period. It is, however, often necessary to obtain digestibility coefficients on rations for which this procedure is not readily applicable, either owing to limited time or to the nature of the ration to be fed. Hence the advantages of a system that obviates consideration of previous diets and the strict confinement of animals to cages to permit the accurate weighing of food and faeces, and includes the possibility of assessing the direct digestibility of pasture herbages under grazing conditions.

In 1926 Bergeim [2] suggested a modified procedure for determining the apparent digestibility of food, depending upon the elimination of a suitable constituent of the food with practical completeness in the faeces. The digestibility coefficient may then be calculated from the relationship,

$$\text{Dig. coeff. } \% = 100 - 100\,\frac{a \times n \text{ in food}}{b \times n \text{ in faeces}}$$

where a, b, and n represent respectively percentage of the constituent in food, of the constituent in faeces, and a specific nutrient in either food or faeces.

Heller, Breedlove, and Likely [3] used the normal iron-content of a ration as the key substance. The use of silica, naturally contained in the food, was proposed by Gallup and Kuhlmann [4]. Their critical investigation [5] suggested an appreciable metabolism of naturally occurring silica, and its subsequent elimination through other channels.

It is generally agreed that lignin forms the least digestible part of herbage. From the chemical point of view, and its classification biologically, the role of lignin is most difficult to assess because its constitution is uncertain. The literature abounds with analytical methods for determining lignin, methods which, however, do not give comparable yields, or afford reliable criteria for assessing either the purity of the product or the extent of its recovery. Ellis, Matrone, and Maynard [6] have assumed that lignin is non-metabolizable, and have recently suggested the use of the lignin of the ration as a suitable 'marker'.

In the present paper a comparison is made of the recovery of naturally occurring reference substances that have been proposed for use in

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modified digestibility procedures; and the applications of such procedures to digestibility studies is considered.

Experimental

Two does of the same litter were fed on a dry mash consisting of 40 parts oats, 40 pts. maize, 10 pts. bran, 5 pts. white fish-meal, and 5 pts. dried grass (by weight). One per cent. of cod-liver oil was incorporated to ensure a sufficiency of vitamins A and D. The experimental period of 7 days was preceded by a pre-collection period of 6 days during which the animals became accustomed to the cages and food.

Analytical Methods

Lignin was determined by two methods:

(*a*) Norman and Jenkins [7, 8]. One gram of material which had been extracted with a benzene-alcohol mixture was dried, refluxed for 1 hr. with 5 per cent. sulphuric acid, again dried, and treated with 72 per cent. sulphuric acid in the cold. The concentration was then reduced to 3 per cent., the material boiled under the reflux for 2 hrs., filtered, dried at 100° C., and weighed. The loss on ignition of the residue gave the lignin.

(*b*) Crampton and Maynard [9]. After thorough extraction with ether, the material was digested for 12 hrs. with 2 per cent. pepsin in N/10 hydrochloric acid at 40° C., and then brought into solution in formaldehyde and concentrated sulphuric acid, the lignin being subsequently recovered by precipitation in water, and granulated with a mixture of chloroform and acetic acid. The residue was dried at 110° C. and the lignin determined by loss on ignition.

Silica was determined by the procedure given by the A.O.A.C. (1935, p. 6).

Iron.—From 0·5 to 1 gm. of material was 'ashed' at a temperature below 600° C. The silica was dehydrated with conc. hydrochloric acid and the iron extracted with 2N.HCl. The iron was determined by the intensity of the violet colour developed on the addition of thioglycollic acid, using a Spekker absorptiometer. A standard iron solution was used to calibrate the instrument.

Digestible nutrients.—The food and faeces were analysed by the procedures of the Fertilizers and Feeding Stuffs Regulations, 1932.

Results

The results are presented in Tables 1, 2, and 3.

Discussion

Considering the methods for lignin (Table 2), it is apparent that the two procedures are not comparable. In every case the method of Crampton and Maynard gives the higher result. The difference is much greater for food than for the faeces, being approximately 15 per cent. in

TABLE 1. *Analyses of the Food and Faeces*

	Rabbit	
	A	*B*
Food eaten, gm.	807·5	851·3
Dry faeces, gm.	214·3	234·2

Constituent	*Feed*			*Faeces, Rabbit A*		*Faeces, Rabbit B*	
	Refused (%)	*Offered* (%)	*Moisture-free* (%)*	*Per cent.*	*Moisture-free* (%)	*Per cent.*	*Moisture-free* (%)
Dry matter	87·79	87·75	100·00	96·03	100·00	98·06	100·00
Moisture	12·21	12·25	0·00	3·97	0·00	1·94	0·00
Ether-extract	5·54	5·65	6·44	2·04	2·12	2·44	2·49
Crude protein	14·90	14·84	16·91	17·63	18·35	17·30	17·64
Ash	3·31	3·30	3·76	8·71	9·07	9·16	9·34
Crude fibre	6·80	6·71	7·65	21·83	22·73	21·30	21·72
N-free extractives	57·24	57·25	65·24	45·82	47·73	47·86	48·81

* These figures refer to the feed offered.

TABLE 2. *Recovery of 'Reference' Substances*

Reference Substance	*'N. & J.' lignin*		*'C. & M.' lignin*		*Silica*		*Iron*	
Rabbit	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*
Food intake, gm.	807·5	851·3	807·5	851·3	807·5	851·3	807·5	851·3
Constituent, %	3·65	3·65	4·23	4·23	0·68	0·68	0·020	0·020
Consumption, gm.	29·47	31·07	34·16	36·01	5·49	5·79	0·1615	0·1703
Faeces output, gm.	214·3	234·2	214·3	234·2	214·3	234·2	214·3	234·2
Constituent, %	13·52	12·70	14·60	13·94	2·49	2·58	0·0594	0·055
Output, gm.	28·97	29·74	31·29	32·65	5·33	6·05	0·1272	0·1290
Balance, gm.	+0·50	+1·33	+2·87	+3·36	+0·16	−0·26	+0·034	+0·041
RECOVERY, %	98·3	95·7	91·6	90·7	97·1	104·5	78·8	75·8

TABLE 3. *Comparison of the 'Modified' and Conventional Digestibility Coefficients*

Constituent	*Digestibility coefficient, per cent.*				
	Procedure				
		Modified			
	Conventional (7 days' period)	*'N. & J.' lignin*	*'C. & M.' lignin*	*Iron*	*Silica*
Rabbit A					
Dry matter	69·8	69·2	67·0	60·0	68·9
Ether-extract	90·1	91·9	89·1	86·8	89·8
Crude protein	67·2	66·6	64·2	56·6	66·2
Crude fibre	10·2	8·6	1·9	−18·8	7·5
N.F.E.	77·9	77·5	75·9	70·7	77·2
Rabbit B					
Dry matter	68·7	67·3	65·5	58·6	70·0
Ether-extract	88·1	87·3	86·6	84·0	88·4
Crude protein	67·3	65·8	64·0	56·8	68·7
Crude fibre	10·7	7·0	2·0	−17·7	14·7
N.F.E.	76·6	75·5	74·2	69·0	77·5

the former and 8 per cent. in the latter. Since an enzyme pre-treatment can be expected to remove very little, if any, of the hemicellulose, it would suggest that the high results of the Crampton and Maynard procedure are due to the presence of excesses of carbohydrate material, mainly pentosan, and perhaps even of protein, which have been shown by Norman and Jenkins [7, 8] to lead to high results. This suggestion finds further support in view of McAnally's findings [10] that the dietary cellulosans and pentosans are more readily fermented in the intestine than cellulose. This would account for the closer approximation of the results for the faecal matter obtained by the two methods. These results suggest that the Crampton and Maynard method is not suitable for determining lignin in feeding experiments.

Considering the lignin balances, there is a difference of about 6 per cent. between the two methods, and the recovery of 98·3 and 95·7 per cent. of lignin by the method of Norman and Jenkins is almost complete. This is in agreement with the work of Ellis *et al.* [6]. However, the method of Norman and Jenkins is itself open to criticism as Sen Gupta has recently shown [11] that some lignin is soluble in the 5 per cent. sulphuric acid of the pre-treatment.

The recovery of silica is good but variable between the two animals. Although the figures of 97·1 and 104·5 per cent. can be accepted as showing a complete balance, such variable figures are not satisfactory from the physiological point of view, as they would indicate an uncertain metabolic path for silica. The recovery of iron is very low indeed under the present experimental conditions. Much work has been done to show that iron has a very complex metabolism in the animal organism [12], and its use must therefore be limited.

The conventional digestibility coefficients, calculated from the data in Table 1, are given in Table 3. The coefficients using the modified technique have been calculated from the data in Tables 1 and 2 and the results are given in Table 3. These figures show that only the 'lignin ratio' method, using Norman's method for the estimation of lignin, and the 'silica ratio' method give results comparable with those of the conventional method.

Under the conditions of a pasture study, there is always the danger that silica from the soil may contaminate the food and faeces analysed, and this consideration, together with those discussed earlier, seriously limits its use.

The results obtained by the use of iron are very low indeed and present an entirely erroneous picture of the digestibility of the ration. It is apparent that where the digestibility of a nutrient is of a low order of magnitude, the calculated digestibility coefficients would tend to deviate appreciably from those obtained by the conventional method.

Summary

The use of modified procedures in digestibility studies has been investigated, using lignin, silica, and iron as reference substances. The results demonstrate that the estimated recovery of lignin depends on the method employed for its isolation, and show that if one of the criteria

of an analytical method for determining lignin be taken as the extent of its recovery from the faeces, the lignin isolated by the 72 per cent. sulphuric acid method of Norman and Jenkins has much to commend it.

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BACK-CROSSING FOR RESISTANCE TO STEM RUST OF WHEAT IN SOUTH AUSTRALIA

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WITH PLATE 8

Stem rust in South Australia.—PERIODIC epidemics of stem rust (*Puccinia graminis tritici*) have always been a feature of wheat-farming in South Australia. Records reveal that rust attacked crops as early as 1854 and later references indicate that the incidence of epidemics was often rather severe. During the past 10 years losses have been serious on three occasions. Reductions in yield have been estimated at 10 million bushels in 1941 and at 4 m. bu. in each of the years 1946 and 1947.

All the commercial varieties grown before 1941 were quite susceptible to rust, but the epidemic of that year very clearly demonstrated the value of some cross-breds derived from the American wheat Hope. One of these—Nabawa × Hope cross—was so outstanding that it was immediately released to farmers under the name Warigo [1]. Its popularity with farmers was so great that by 1947 it ranked as the second leading wheat of the State, being sown over 175,000 acres in that year. This, the first truly resistant variety in South Australia, has been followed by others, such as Gabo, Kendee, Charter, Celebration, and Yalta from New South Wales, and Glenwari released last season in South Australia.

Waterhouse [2], in his analysis of the identity and distribution of the physiologic races of *P. graminis tritici* in Australia, has shown that race 34, which first appeared in 1926, had become the most important race by 1929, when it completely superseded the other races. It has remained predominant ever since. Waterhouse and Watson [3], in distinguishing the Australian race 34 from cultures of race 34 obtained from the United States, adopt the term 'biotypes' as descriptive of these two entities. In 1942 these workers [4] identified an additional biotype of race 34 from New South Wales, characterized by an ability to infect the variety Eureka. This variety derives its resistance from Kenya C6040, and, although susceptible to the new biotype, was, and still is, resistant to the old Australian biotype of race 34. The new Eureka-attacking biotype was first detected in South Australia in 1943 [4].

Background to the present work.—Facilities for testing new varieties in yield trials in country districts of South Australia are rather limited, and for this reason it has not always been easy to assess their regional adaptability. Furthermore, many of the old standard varieties such as Bencubbin, Ranee, and Dundee, as well as the newer wheats Ridley, Javelin, Dirk, Seewari, Scimitar, and Rapier, although susceptible to rust possess many valuable inherent qualities—qualities that have been synthesized through the painstaking efforts of breeders in past years.

With these two thoughts in mind it was felt that future breeding work for rust-resistance might better be approached through back-crossing rather than through the continued use of the standard pedigree method of breeding.

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The genetic basis of stem-rust resistance in the Kenya wheats has been the subject of a number of studies (*vide* Macindoe [5] and Watson and Waterhouse [6]). In 1945 Watson and Waterhouse recognized three independently inherited genes, one occurring in each of the following Kenya wheats:

1. Kenya 743 (C6040): the parent variety of Eureka.
2. Kenya 744 (C6041).
3. Kenya 745 (C6042): this same gene also occurs in Gabo, a wheat deriving its resistance from the durum variety Gaza. The genes in Kenya 744 and Kenya 745 are effective in controlling both biotypes of Australian race 34, but that in Kenya 743, although effective against the old or standard Australian race 34, fails to control the new Eureka-attacking biotype.

With regard to the back-crossing procedure reference should be made to Harlan and Pope [7] who, in 1922, pointed out the probable value of back-crossing in small-grain breeding. In 1935 Miles [8] brought the method to the attention of Australian plant-breeders. Briggs [9] has very clearly demonstrated its application in adding the bunt-resistance of Martin to some commercial wheat varieties in California. The practical achievements of Briggs and his colleagues have attracted widespread interest, for they serve to illustrate how a sound breeding-programme can be put into operation once the breeder possesses the necessary information regarding the various 'resistant' genes and their relationship to the predominant physiological races of the pathogen that may occur in any particular region.

The back-crossing procedure.—The programme for incorporating 'resistant' genes in South Australian wheats by back-crossing was started in 1942. Nine wheats, which were either widely grown at that time or which showed distinct promise as new varieties, were selected as the recurrent parents. They were: Bencubbin, Dirk, Dundee, Javelin, Ranee, Rapier, Ridley, Scimitar, and Seewari. In 1944 the programme was extended to include a promising cross-bred from Victoria (subsequently released as Insignia).

The original plan was designed to carry through two parallel series of back-crosses using each of the two genes present in Eureka and Gabo respectively. However, with the appearance of the Eureka-attacking biotype of Australian race 34 in 1943, the Eureka derivatives then became quite susceptible and were discarded. The Gabo series remained resistant to both the old and new biotypes and were carried through to completion in 1948.

The Gabo gene for resistance in the heterozygous condition is almost completely dominant, and there has never been any difficulty in identifying the heterozygous plants of the segregating population in either the seedling or mature stages of growth.

As so few plants were needed during the actual back-crossing procedure, they occupied very little space and it was possible to grow 2 to 3 generations each year. To achieve this it was necessary, first to provide extra illumination during the short days of winter, and secondly to

hasten ripening by harvesting prematurely. Although freshly harvested seed was sometimes slow to germinate, this difficulty was insignificant by comparison with that experienced in a similar back-cross programme with barley.

During the summer months the plants were grown outside under irrigation and under such conditions stem rust always developed rapidly following hypodermic-needle inoculation of susceptible plants with a uredospore suspension. At other times of the year the plants were grown in the greenhouse where seedling inoculation with rust was the standard procedure.

The heterozygous resistant plants chosen for crossing to the recurrent parent were random selections from the 1 : 1 segregating generation and, as a rule, only 2 such crosses for each variety were made; this provided adequate crossed seed to ensure that at least 2 or 3 resistant segregates were obtained in the following generation. An endeavour was made to use the susceptible recurrent parent as the female in each of the crosses. Special care was taken to ensure that the recurrent parent strain used was typical for that variety, for it must be emphasized that on this depends the successful recovery of the genotype of the recurrent parent.

An example may perhaps indicate a little more precisely the detailed procedure adopted in transferring a 'resistant' gene to the variety Insignia by back-crossing. In this instance it was attempted to carry the project through as rapidly as possible, at the same time establishing a time schedule that could be followed in future years.

Although Insignia was not named and released by the Victorian Department of Agriculture until 1946, its excellent performance in yield trials conducted in Victoria up to 1944 justified the view that the variety might ultimately establish itself in the wheat areas of South Australia. This cross-bred (Ghurka × Ranee M. 6173T 14–2–1–1) was generously made available by the Victorian Department of Agriculture in 1944 and immediate steps were taken to incorporate resistance to stem rust by back-crossing.

Insignia, as the cross-bred was later to be known, was sown on November 20, 1944, and crossed to Gabo on January 18, 1945. Then followed:

(i) F1 (Insignia × Gabo) sown March 7, 1945, and crossed to Insignia as the first back-cross on June 4, 1945.

(ii) The F1 of the first back-cross (Insignia × Gabo)^1 × Insignia sown on July 23, 1945, and resistant segregates crossed to Insignia as the second back-cross on November 7, 1945.

(iii) The F1 of the second back-cross (Insignia × Gabo × Insignia)^1 × Insignia sown January 22, 1946, and resistant segregate crossed to Insignia as the third back-cross on March 12, 1946.

(iv) The F1 of the third back-cross (Insignia × Gabo × Insignia × Insignia)^1 × Insignia sown June 1, 1946, and resistant segregates crossed to Insignia as the fourth and final back-cross on September 27, 1946.

(v) The F1 of the fourth back-cross Gabo × Insignia[5] sown December 21, 1946, selfed and resistant segregates harvested in February 1947.

(vi) The resultant resistant F2 plants of Gabo × Insignia[5] sown March 1, 1947, selfed and harvested in June 1947.

(vii) F3 families of Gabo × Insignia[5] sown July 11, 1947, and one homozygous resistant family selected for bulking as the new strain.

(viii) The new rust-resistant strain sown as a bulk plot on December 20, 1947.

The time then, from the sowing of the original parental varieties (Nov. 1944) to the bulking of the F3 seed of the fourth back-cross (Nov. 1947) was 3 complete years. To this must be added an extra period to allow for further testing and multiplication of the seed prior to its commercial release.

The above procedure was essentially that adopted for the remaining 9 varieties, although in some instances only 3 back-crosses were made. On some occasions the new back-crossed strain was built up from 3 or 4 bulked homozygous F3 lines.

Results

At the end of the 1948 season supplies of seed of 9 of the 10 new strains were sufficiently large to warrant their release to farmers. Each new strain had been grown alongside its respective prototype for the 3 seasons 1946–8. Stem-rust epidemics in 1946 and 1947 provided excellent opportunities for demonstrating the superiority of the new strains under such conditions, whilst the general similarity between the new and old strains in both agronomic characteristics and yield-potential was evident in the rust-free year of 1948.

The rules governing the nomenclature and registration of Australian wheat varieties were amended in 1947 to permit the use of a numerical suffix for strains evolved by back-crossing. This practice is in conformity with Californian procedure in which the name of the recurrent parent is retained with an added suffix indicating the year in which the new strain was produced.

Up to the present the 8 strains released are: Bencubbin 48, Dirk 48, Dundee 48, Javelin 48, Rapier 48, Ridley 48, Scimitar 48, Seewari 48.

In 1940 Ranee was the wheat most widely grown in the State, but owing to its susceptibility to stem rust it has recently lost favour, ranking fourth in 1947. To a large extent this decline could have been arrested by the release of Ranee 48. However, both Ranee and Ranee 48 possess poor inherent baking quality, and because an attempt is being made to raise the general quality level of South Australian wheat, it was deemed inadvisable to release Ranee 48. Other superior new varieties, such as Ridley 48, could be expected to replace Ranee, so that in reality the breeder has been able to exercise some measure of control through his choice of varieties in the back-cross programme.

Discussion

Back-crossing finds its greatest application in crop improvement when it is desired to rectify single faults in varieties otherwise acceptable.

Australian wheat varieties have constantly improved during the past 60 years. Yield and drought-resistance have always been the main considerations and, particularly in more recent years, flag-smut resistance and improved baking quality have resulted from the widespread use of the pedigree or pure-line method of breeding. Although this approach will continue to lead to the production of new superior varieties there is little doubt that the small improvements expected will become increasingly difficult to secure in the future. The assessment of significant yield increments and the determination of regional adaptability of new varieties in South Australia is a much more difficult process to-day than it was 20 years ago.

Since disease-resistance has so frequently a simple genetic basis it is admirably suited to the back-crossing technique and its application to wheat-breeding in South Australia will permit the consolidation of the progress made over the past years; and this in a simple and economical manner.

An important feature in adding disease-resistance through back-crossing is the fact that it is possible to counter any change in the composition of the population of the physiologic races in an area by adding a second or third gene to that already incorporated. This, of course, presupposes that such genes are available. It has been shown that this process need take no longer than 3 years, so that if the breeder possesses an adequate knowledge of the available 'resistant' genes and their relationship to the known races of the pathogen concerned, he is in a position to add additional genes to those already existing should the necessity so arise. Stem rust of wheat has been much investigated in many countries, but an important gap in our knowledge of gene-race relationships remains, and this is perhaps the greatest handicap to effective breeding for resistance to this disease. The physiological races of *Puccinia graminis tritici* continue to be classified on the basis of a rather arbitrarily chosen list of differential varieties, and the substitution of these varieties by others possessing known single genes would be of great help to the plant-breeder.

More effective use of back-crossing would be possible if two aspects of procedure could be clarified. In the first instance more precise information is needed on the number of back-crosses necessary to be reasonably sure of recovering, for all practical purposes, the genotype of the recurrent parent. Californian workers have used 4 to 6 back-crosses, but experience in South Australia so far indicates that little is gained by making more than 4 back-crosses. Experiments have been designed and the necessary crosses made in order to secure material for an investigation of the trends in both yield and baking quality during the progressive stages of the back-cross programme.

Secondly, an examination should be made of the relative merits of the Californian procedure of making a rather large number of crosses in

each back-cross generation and the final merger of a number of F_3 lines as compared with the procedure outlined above in which few crosses are made and the final strain is derived from a restricted number of homozygous F_3 families. These considerations have been fully discussed by Knight [10] in an account of the back-cross technique as applied to cotton breeding.

Summary

The back-cross method of breeding has been used to transfer stem-rust resistance from the wheat variety Gabo to 10 South Australian varieties.

Effective application of the method is dependent upon a knowledge of the genes available and their relationship to the locally occurring races of *Puccinia graminis tritici*.

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FIG. 1. Susceptible and resistant segregates in the field, March, 1944

FIG. 2. Susceptible and resistant segregates in the greenhouse, May, 1945

THE BREEDING OF DISEASE-RESISTANT VARIETIES OF OATS

Part I. PHYSIOLOGIC RACES, DISEASES, AND PESTS

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THE systematic improvement of oats by the method of hybridization is a comparatively recent development, and in the main dates back to the rediscovery of Mendel's interpretation of segregation in plant hybrids at the beginning of the present century. Although the hybridization method in its early phases was applied chiefly to the production of new varieties with superior yields of grain, improved stiffness of straw, and other morphological and physiological characters, evidence was rapidly developed, by the study of hybrid material and single-plant selections derived from land varieties and new introductions, which showed that the resistance or susceptibility of plants to fungal disease behaved as a varietal character. Examples of some of the earlier varieties carrying resistance to fungal diseases and obtained by single-plant selection are Albion, Richland, and Iogold developed by Burnett [1] at Ames, Iowa, which are resistant to stem rust, and S.75 *Ceirch Llwyd*, a diploid variety highly resistant to loose and covered smut developed by selection from a composite stock of *Avena strigosa* at Aberystwyth [2].

It was not until Biffen [3] discovered that resistance to yellow rust in wheat is inherited as a Mendelian character, in the same manner as morphological and physiological characters are inherited, that the possibility of incorporating resistance to disease by the method of hybridization came to be regarded as a practical breeding proposition.

In countries such as the United States, Canada, and Australia, where the prevalence of crown rust, stem rust, loose and covered smuts causes heavy annual losses, and occasionally in some areas may cause complete failure of the crop, systematic breeding for resistance to disease has now become an integral part of the crop-improvement programme at all breeding stations. Losses caused by fungal disease in most European countries are, however, smaller and more spasmodic in their occurrence. In the western and south-western parts of Britain damage to the yield and quality of the grain often occurs on upland farms in seasons favourable to the development of rust, and especially in the late-sown crops.

Physiologic Races

In much the same manner as the systematic study of the different oat species has revealed the presence of a wide diversity of naturally occurring forms differing in adaptability to environmental conditions, so also have critical and extended studies demonstrated the great diversity of forms which exist within each specific group of fungal parasite. Since Eriksson [4] and Eriksson and Henning [5] in 1894 drew attention to the fact that pathogenic fungi varied in their ability to attack different

or related species of plants, very considerable advances have been made in our knowledge of the nature and behaviour of parasitic organisms. We now know from the fundamental investigations of Stakman [6, 7]; Stakman and Piemeisel [8]; Craigie [9]; Newton, Johnson, and Brown [10], and others [11, 12, 13, 14], that the stem-rust species *Puccinia graminis* (Erikss. and Henn.) consists not only of a number of varieties (the 'formae speciales' of Eriksson) each restricted in the degree to which it can attack certain genera of the family Gramineae, and which were regarded by Eriksson as the ultimate units of specialization, but that each of these varieties may comprise a number of physiologic races, each more narrowly restricted in the degree to which it can attack different varieties of the same plant species. Although these physiologic races may not be distinguishable on morphological features, except that some may differ significantly in the size of the uredospores [15, 12], their individuality is clearly demonstrable by their characteristic types of infection when inoculated on a series of differential host varieties. Most of the evidence so far obtained shows that physiological characters in pathogenic fungi are at least as stable as morphological characters [7], and although subject to environmental conditions, as are other plant characters, there is no convincing proof that the effects of environment cause any fundamental change, the modifications in their pathogenicity being phenotypic rather than genotypic in character. These discoveries are of the greatest practical importance to the plant-breeder concerned with the development of new varieties resistant to fungal diseases.

Parasitic Diseases

Of parasitic diseases which attack oats in Britain the most important are stem rust (*Puccinia graminis* var. *Avenae* Erikss. and Henn.), crown rust (*Puccinia coronata* var. *Avenae* Corda), loose and covered smuts (*Ustilago* spp.), leaf-spot and seedling blight (*Helminthosporium Avenae* (Bri. and Car. Eid.), mildew (*Erysiphe graminis*, DC.), and root-rots. The root-rots are caused mainly by *Ophiobolus graminis* var. *Avenae* (Sacc.) E. M. Turner, *Pythium*, *Fusarium*, and *Corticum* (*Rhizoctonia*) *Solani* spp. Some damage is also caused by grey leaf or grey speck [16]. Appreciable damage may be caused by plant pests such as wireworm (*Agriotes lineatus*), frit-fly (*Oscinella frit*), and leather-jackets (*Tipula oleracea*), and in some areas injury may be induced by localized attacks of stem eelworm (*Anguillulina dipsaci*) and root-eelworm (*Heterodera schachtii*), when the weather conditions in spring are unfavourable to crop-growth.

Stem rust.—In the study of numerous samples of stem rust of oats collected in the U.S.A., Canada, Sweden, and South Africa, Stakman, Levine, and Bailey [11], using the oat varieties Victory, White Tartar, and Monarch Selection as differential hosts, demonstrated the presence of four physiologic races. Other investigators [17, 13, 18, 19, 20] have identified additional races, bringing the total number discovered in different countries to 13, or possibly 14, races.

Crown rust.—Hoerner [21] in 1919 distinguished the presence of four physiologic races in collections of crown rust, using as differential hosts the two oat varieties Ruakura and Green Russian. More recently,

investigators in the U.S.A. and Canada [22, 23, 24] in inoculation tests with crown-rust samples collected over a wide geographical area, and using a larger number of differential host varieties, have identified additional races. Brown [25] observed the occurrence of three races in samples collected in Britain, and Frenzel (quoted by Murphy [23]) distinguished 33 races in collections made in Germany. According to Peturson (quoted by Johnson and Newton [26]) no fewer than 82 physiologic races of crown rust have been identified up to the year 1946 on the basis of their reactions on 11 standard host varieties.

The infection types in both species of rust are on some of the host varieties found to differ somewhat with the temperature and other conditions under which the inoculation tests are made, at least in respect of some of the physiologic races studied [27, 28, 29, 23], certain races showing a tendency to increased virulence at higher temperatures. Control of the temperature and light at appropriate levels is essential in order to ensure uniform and typical reactions, and the use of pure-seed stocks of the accepted and requisite number of standard varieties used as differential hosts for race identification are equally important factors in securing comparable and conclusive data on host reactions.

Loose and covered smuts.—The existence of physiologic races in both loose and covered smuts was discovered in America in 1924 by Reed [30], and in Wales in 1925 by Sampson [31]. In subsequent studies Reed [32] demonstrated the existence of 29 physiologic races of *Ustilago Avenae* and 14 of *U. Kolleri*. Seventeen host varieties were used for separating the loose smut races, and 10 for the covered. Later work [33] has revealed the existence of 2 additional races of loose smut, bringing the total number now known to 31. Important contributions to our knowledge of the biology of the oat smuts have been made by Johnson [34], Bartholomew and Jones [35], Popp and Hanna [36], Sampson [31, 37, 38, 39], Sampson and Western [40], and Western [41].

Mildew.—That powdery mildew may be subdivided into specialized varieties, each distinguishable by its ability to attack different genera of the cereals and grasses, was first demonstrated by Marchal [42] in 1902. Here too, as in the case of the rusts, subsequent researches by Salmon [43] and Reed [44] have shown that the 'variety' is not the ultimate unit of specialization, and that each variety may comprise a number of physiologic races. There are, however, no recorded investigations of the study of physiologic races of the variety *Erysiphe graminis Avenae*. Recent publications by Cherewick [45] and Newton and Cherewick [46] in Canada have demonstrated the existence of 12 physiologic races in the variety *Hordei*, which attacks barley, and 5 races of the variety *Tritici* on wheat. These authors have added much to our knowledge of the biology of the mildews of wheat and barley—their methods of overwintering, reactions to light, temperature and humidity—and have shown that there is no lack of mildew-resistant material in either barley or wheat suitable for the breeding of new resistant varieties. Their work also indicates that it is possible in these two cereals to combine resistance to mildew with other plant-characters of desirable agricultural value. Breeding experiments at the Welsh Plant Breeding Station at

Aberystwyth have shown that oat varieties react differently to infection by mildew, and whilst some varieties are highly susceptible to attack, others, though not immune, show a high degree of resistance at certain phases of plant-growth. Crosses made between resistant and susceptible varieties demonstrate that resistance to mildew in oats behaves as a Mendelian character, and that high-yielding mildew-resistant varieties with desirable agricultural characters can be produced by the hybridization method (unpublished data).

Leaf-spot and seedling blight.—Unlike *Helminthosporium sativum*, which attacks barley and wheat and is reported by Christensen [47] to comprise a number of physiologic races, the parasitic fungus causing leaf-spot and seedling blight of oats exhibits a low degree of specialization. Most varieties of oats are susceptible to attack, and none of the commonly grown varieties has been found to be resistant [48, 49]. Sampson [50], in observations on 37 varieties, found only one variety, Algerian *sterilis* (*A. byzantina*), free from infection. Fortunately this disease, which to a large extent is seed-borne, can be fairly well controlled by seed-treatment with organo-mercury compounds. A new species of this disease designated *H. victoriae* has recently appeared in the U.S.A. [51], which attacks the variety Victoria and all crown-rust-resistant derivatives of Victoria parentage. It causes marked reduction of grain yield. Partially effective control is said to be obtained by seed-treatment with certain of the improved organo-mercury dusts.

Halo blight (*Pseudomonas coronafaciens* (Elliot) Stapp).—This is a bacterial disease and has not been observed to cause damage on oats in Britain [16]. The varietal reactions of oats to this disease have been studied by Elliot [52], and by Aamodt and Platt [53], who found that varieties differed in their resistance to attack, but none was immune. Banner is reported to be less susceptible than Victory.

Seedling rot and root-rots.—Specialization in the fungi causing root-rots appears to be weakly developed, since few, if any, varieties of oats appear to possess any marked degree of resistance. Experimental work in progress at Aberystwyth seems to indicate that the diploid variety *Ceirch Llwyd Cwta* (S.171) is less susceptible to injury by *Ophiobolus graminis Avenae* than varieties of the common oat group. In the absence of fully resistant varieties an alternative solution to the problem of root-rot diseases may be sought in improved cultivation methods, or by pursuing researches into the ways and means of devising methods of developing antibiotic substances in the soil, as indicated by the experimental work of Grossbard [54] and Simmonds [55]. Some degree of resistance to *Pythium* root necrosis has been observed by Welch [56] in a few oat varieties belonging to the species *A. byzantina*.

Plant pests.—Although most varieties of oats are observed to be attacked by wireworm and leather-jackets, a moderate, or fairly high, degree of resistance to frit-fly attack is present in the varieties Summer, Spet, Hede, and Eagle. Extensive studies of the biology of the frit fly have been made by Cunliffe [57], who observed that resistance is an inherited character, and that three classes were distinguishable amongst the oat varieties subjected to experimental study, viz., resis-

tant, moderately resistant, and susceptible. In later work Cunliffe and Hodges [58] have shown that the varieties resistant to stem-infestation in the juvenile stage owe their low incidence of attack by frit fly to the fact that they are less favoured as hosts for oviposition than other varieties of oats. The marked differences in degree of stem-infestation in the spring as between Victory (susceptible) and Summer (resistant) were, however, not correlated with any resistance to grain-infestation caused by the summer brood of flies, both varieties being about equally susceptible to the latter. Breeding studies with a wide range of crosses between resistant and susceptible varieties of oats have been conducted by Carson at Cambridge: no detailed inheritance data have been collected, but the results are said to be indicative of multifactorial inheritance.[1] According to Scheibe [59], resistance to frit-fly attack is conditioned by physiological factors, among them the capacity of the grain to form cane-sugar.

A well-defined reaction is shown by oat varieties to attack by stem eelworm, although most varieties are susceptible. Goodey [60] in his studies of varietal reactions reports a high degree of resistance to attack in Grey Winter, and also in the bred variety of white winter oats Aberystwyth S.81. Picton, Avoine d'hiver, Unique, Victoria, Capa, and Pampa have also been found by Goodey[2] to be resistant to attack.

Non-parasitic diseases.—A disease of oats known as Grey Speck or Grey Leaf occurs on certain types of alkaline soils, and is caused by a deficiency in the soil of available manganese [61, 62, 63, 64]. Although most oat varieties are susceptible, Fyris, Perle, and Melog III are found to be resistant [65], and so also are Scotch Potato, Radnorshire Sprig, and *Ceirch-du-bach* [66].

Crop failures due to copper deficiency have been reported to occur on calcareous soils along the coast of South Australia [67]. One variety of *Avena strigosa* was found to possess a high degree of resistance and made healthy growth, whereas the Mulga oat was susceptible.

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